

VARIATION IN PINNIPED DENTITION

by

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A THESIS

Presented to the Department of Biology
and the Robert D. Clark Honors College
in partial fulfillment of the requirements for the degree of
Bachelor of Science

September 2018

An Abstract of the Thesis of

Caitlyn Boatman for the degree of Bachelor of Arts
in the Department of Biology to be taken September 2018

Title: Variation in Pinniped Dentition

Approved: _____

Samantha Hopkins

I studied variation in the teeth of 5 different species of pinniped: *E. jubatus*, *Z. californianus*, *P. vitulina*, *E. barbatus*, and *O. rosmarus*. Prior to this study, little work had been done on dental variation in marine mammals with homodont teeth. Most studies have looked specifically at terrestrial carnivores such as *C. lupus* and *F. silvestris*. Specifically, I compared the coefficient of variation of a few different aspects of dentition (total surface area, individual tooth surface area, toothrow length, tooth width and blade length) and compared them to CVs of other published terrestrial mammals. In general, I determined that pinniped dentition was much more variable than dentition of terrestrial species (i.e. had higher CVs). In addition, I determined that blade length, toothrow length, and total surface area is correlated with body size. Larger bodied animals or species have larger surface areas, toothrow lengths, and blade lengths. Even when normalized for body size, variation in mean sizes of each of these aspects persisted, suggesting there is no ideal toothrow length, blade length, or total tooth surface area needed for survival.

Acknowledgements

I would like to thank Professor(s) Samantha Hopkins, Edward Davis, Win McLaughlin and other names thereafter, for helping me to fully examine the specific topic and consider the various perspectives and contexts related to this subject matter. Thank you for all your assistance and guidance throughout the entire project. Thank you to all members of Hopkins lab for extra guidance and assistance. Thank you to Win McLaughlin for assisting in photography specimens. Thank you to the museums FMNH, UWBM, UAM, MNCH, and MVZ for providing specimens. Thank you Chris J. Conroy for allowing me to visit the Museum of Vertebrate Zoology in person and photograph specimens at that location. Thank you to my family, Abby Graham, and Riley Cole for support throughout my college experience.

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Introduction

Warm blooded mammals, because they require a great deal of energy to continually heat their bodies, demand an efficient way to process their food. Crucial to this efficiency are teeth: using teeth, animals can process food and turn it into smaller particles with larger surface areas, allowing easier access and energy extraction for enzymes in the animal's stomach (Ungar 2015). Because of this high energy requirement and the relationship between teeth and proper mastication, tooth structure and shape is intimately connected with the tooth's function and teeth are critical to the evolution of mammals (Ungar 2015). Teeth evolved to efficiently process a specific type of prey and therefore vary in form and function across taxa (Van Valkenburgh 1989; Meiri 2005; Friscia 2006; Popwics 2003). They most typically have complex crowns and are shaped in a way to efficiently process a specific type of food item (Van Valkenburgh 1989; Meiri 2005; Friscia 2006; Popwics 2003). The high degree of selective pressure exerted upon teeth is evidenced by the diversity of dental morphology across species (Valkenburgh 1989). For example, grazers (such as cows, *Bos taurus*) have large, high crowned teeth with enamel ridges that are able to grind up grasses and tolerate wear from grit consumed with food (Gailer 2016). In extant, small mammals, carnivores, insectivores, and omnivores can be identified using the length of carnassial blades and the size of molar grinding areas (Friscia 2006). Carnivores evolved a variety of different tooth forms to deal with differing dietary restrictions, including large blade-like carnassials in Felidae and Canidae for shearing and flat, square, four-cusped molars in Suidae and Ursidae for crushing. (Van Valkenburgh 1989).

Because of their importance in processing food, a wide variety of studies look at variation in different aspects of tooth size and shape in species with relatively specialized, heterodont teeth (Meiri et al. 2005; Miller et al. 2009; Szuma 2000; Gingerich 1979; Dayan 2005; Baryshnikov 2003; Rozhnov 2006). *Vulpes vulpes*, the red fox, for example, has a high degree of variation in teeth that occlude less precisely between the top and bottom tooth (Gingerich, 1979). The carnassial pair (the fourth premolar on the top jaw and the first molar on the bottom jaw) which occlude most precisely, have the least variation, followed by incisors with intermediate levels of occlusion (Gingerich 1979). The third molar, with the simplest occlusion, has the highest variation and is sometimes absent entirely (Gingerich 1979). We can see similar patterns of low variation correlated with degree of use in mastication and precision of occlusion with the bottom tooth in other terrestrial carnivores, including species in the families Felidae and Ursidae (Meiri et al. 2005; Miller et al. 2009; Szuma 2000; Gingerich 1979; Dayan 2005; Baryshnikov 2003; Rozhnov 2006).

Coefficients of variation (CV) are a way to quantify variation while removing the effect of absolute size. Terrestrial mammals typically have relatively low CVs in teeth that occlude very precisely, such as carnassials, compared teeth that need not occlude precisely and have relatively low complexity, such as canines (Meiri 2005).

CVs in certain species of canid and felid are consistently low. CVs of individual tooth lengths in *Canis lupus* vary from 3.68 to 8.83 with some of the lowest CVs found in measurements on the fourth premolar (the carnassial) (Dayan 2002). The first and second molar, two more teeth that precisely occlude with their corresponding lower tooth, also have some of the lowest CVs. Comparatively, the lengths of the pre-molars

P¹, P², and P³ have higher CVs (Dayan 2002). CVs for the wildcat species *Felis silvestris*, calculated in this same study are variable but often low. Like *Canis lupus*, the calculated CV for carnassial length (the fourth premolar on the upper jaw) in *F. silvestris* tend to be lower than some other premolars and molars, such as the second premolar and the first molar (Dayan 2002). *F. silvestris* also appears to follow the same pattern of high variation in less complex teeth that do not precisely occlude with bottom teeth and low variation in teeth that have complex shapes and crowns. Both of these species demonstrate relatively low CV scores (though some length measurements in *F. silvestris* can have high CVs, such as the length of the second premolar which has a CV of 25.2).

Ursids, members of the infraorder Arctoidea, also including Pinnipeds and Musteloids, tend to have intermediate levels of variation. Ursids, unlike either canids or felids, tend to be generalized omnivores with large, flattened, four-cusped molars with simplified crowns used for grinding (Miller 2009). The carnassial has been reduced and the other premolars are small and sometimes absent (Miller 2009). In the species *Ursus americanus* (the black bear), CVs ranged from 4.0 to 9.0, depending on the aspect and the sex of the animal and averaged 5.0 to 6.5 (Miller 2009). CVs for different tooth aspects in the cave bear *Ursus spelaeus* were similar to CVs for *U. americanus*, with many CVs between 5.0 and 8.0 (though some aspects had CVs of around 11.0) (Baryshnikov 2003). In general, these terrestrial carnivores (*U. americanus*, *U. spelaeus*, *F. silvestris*, and *C. lupus*) have similar levels of variation ranging from the 4.0 to 8.5 with some outliers, though measures in more precisely occluding, complexly crowned teeth are more variable in bears than other terrestrial carnivores (Miller 2009).

Musteloids, the other non-pinniped member of infraorder *Arctoidea*, also typically have low CV values. A study on pine martens (*Martes martes*) and beech martens (*Martes foina*) determined CVs for two tooth characteristics: length of the lower canine and length of lower first canine. CVs for these two aspects were consistently low across the different examined species and were often within the 2.0-4.0 range (Reig 1992). Another species, the marbled polecat *Vormela peregusna*, has similarly low CVs, ranging from 4.5-4.6 for the four premolar (Miller 2009; Rozhnov 2006). Musteloids tend to have low variation, similar to felids and Canids, and Ursids tend to have intermediate levels of variation (Miller 2009).

Though researchers have studied variation in terrestrial carnivores with heterodont teeth, comparatively little attention has been paid to aquatic carnivores with homodont teeth. Pinnipeds, a clade of marine mammals, have simplified, undifferentiated wedge-like molars and premolars with relatively simplified cups (Churchill 2015a; Adam & Berta 2002).

Ancestral pinnipedimorph dentition, found in some members of the stem group *Enaliarctos* such as *Enaliarctos barnesi*, is heterodont with blade-like cusps on the upper fourth premolar and lower first molar, forming a carnassial pair (Berta 2018). Other species in the group demonstrate a trend towards a decreasing of shearing surfaces on those teeth, later leading to the simple, homodont cheek teeth of modern pinnipeds (Berta 2018; Churchill 2015a).

Modern day pinnipeds have undifferentiated premolars and molars, unlike terrestrial carnivores, which typically have teeth that are shaped to perform different functions (back molars for crushing, carnassials and premolars for shearing) (Van

Valkenberg 1989; Meiri 2005, Evans 2007; Friscia 2006; Popwics 2003). In addition, most pinnipeds do not have occluding cheek teeth (their teeth do not touch when the animal closes its mouth; Adam 2002). Because of their lack of differentiation, the premolar and molar teeth that make up the toothrow are referred together as postcanines. Similar loss of differentiation in the postcanine toothrows is observed in other species of marine mammal, including some members of the order Cetacea and may due to a mutation in the *BMP4* gene during development (Churchill 2015a; Armfield 2013). Loss of differentiation is associated with a loss of mastication of prey items because mastication in water is typically energetically costly (Churchill 2015a; Adam 2002).

Pinnipedia is comprised of three different families: Otariidae (the eared seals, characterized by external earflaps), Phocidae (true seals, characterized by their inability to turn their back flippers forward), and Odobenidae (Walrus, characterized by enlarged upper canines; Berta 2018). Pinnipeds have a fossil record extending back into the late Oligocene with *Enaliarctos* representing the oldest stem pinniped (Berta 2018).

All studies agree that pinnipeds are members of the carnivoran clade Arctoidea, also containing Mustelids and Ursids; however some debate exists on the evolutionary history of the clade with some advocating for a monophyletic origin and others advocating for a diphyletic origin. Some paleontological and morphological studies support diphyletic origin, with sea lions most likely arising from Ursidae and true seals arising from Mustelidae (Kortjesky 2016; Tedford 1976). In contrast, other morphological and molecular studies support monophyly, with pinnipeds most closely related to either

Ursidae or Mustelidae, depending on the specific study (Berta 2018; Agnarsson 2010; Arnason 2007; Dasmahapatra 2009; Higdon 2007; Sato 2006).

Modern pinnipeds employ four different methods for capturing and consuming food, none of which involve chewing (Adam 2002). As a consequence, teeth are not used for mastication in any living species of pinniped. Modern pinnipeds do not capture prey they have to chew, but instead capture prey items they can swallow whole. Pierce feeding is the most common method and involves using the postcanine teeth to bite and hold the prey until the prey can be swallowed whole (Adam 2002). Another common feeding strategy is suction feeding, where the animal opens its mouth to create a gradient in water pressure, thus generating a suction that moves water and prey items into the animal's mouth (Adam 2002). The final two strategies, filter feeding and grip and tear, are considerably less common and are only found in crabeater seals (*Lobodon carcinophagus*) and the leopard seal (*Hydrurga leptonyx*) respectively. Teeth in filter feeders have complicated, lattice-like cusps to filter krill out of the water (Adam 2002). Grip-and-tear feeders use their teeth to take bite-sized chunks out of larger sized prey (Adam 2002). Although pinnipeds exhibit a variety of different feeding strategies, none of those strategies rely on teeth for chewing.

Researchers so far have focused primarily on terrestrial carnivores with teeth used for food processing in studying variation in tooth size and shape (Meiri et al. 2005; Miller et al. 2009; Szuma 2000; Gingerich 1979; Dayan 2005; Baryshnikov 2003; Rozhnov 2006). I studied variation in tooth size and shape in five different species of pinniped with homodont, non-occluding cheek teeth. By studying these carnivores, I hope to determine if the pattern in terrestrial carnivores, of low variation in complexly

crowned teeth, is consistent in marine mammals as well. Because pinniped teeth are not needed to break down food items and because they do not occlude, I would expect these pinnipeds to have much higher variation in different aspects of their dentition than terrestrial carnivores with teeth that are used to process prey and that do, as a consequence, have more upper/lower tooth pairs with very high degrees of occlusion and complicated crowns. Because the consequence of having teeth of varying sizes is greater in animals where the teeth need to occlude very precisely, I would expect pinnipeds to have much more variable teeth, both within species and across species.

I included species that use pierce feeding, suction feeding, or a combination of both. The California Sea Lion (*Zalophus californianus californianus*), subspecies Galapagos Sea Lion (*Zalophus californianus wollebaeki*), and Harbor Seal (*Phoca vitulina*) use pierce feeding exclusively (Adam & Berta 2002). The walrus (*Odobenus rosmarus*) and Bearded Seal (*Erignathus barbatus*) use suction feeding exclusively (Adam & Berta 2002). The Steller Sea Lion (*Eumetopias jubatus*) utilizes both suction and pierce feeding depending on the prey it captures (Adam & Berta 2002). In these species, I will examine the level of variation in different aspects of dental morphology, including the width of each individual tooth, the overall “blade length” for an individual, the surface area of each tooth, the overall total surface area for an individual, and the toothrow lengths for an individual (see methods section for further description of each aspect).

I will examine the extent of variability in these five species in the five different aspects of dental morphology described above and, for some aspects, how that variability is distributed. I expect that these species, because of their undifferentiated,

less complexly crowned, non-occluding teeth, will have more variable dentition than species with more complexly crowned teeth, such as Canids or Ursids. Further, I will determine if the mean values for toothrow length, blade length, and total surface area differ across species. Because pinnipeds employ similar feeding methods and capture similar types of prey (fish and small invertebrates), it may be that there is an ideal toothrow length, blade length, and/or total surface area needed to properly capture prey. If there is an ideal toothrow length/blade length/total tooth surface area to capture prey, I would expect the means of each of those aspects to differ little across species.

Methods

Specimen Collection

Specimens were collected from three different museums: the Museum of Vertebrate Zoology at Berkley (MVZ), the Museum of Natural and Cultural History at University of Oregon (MNCH), the University of Alaska Museum (UAM), the Field Museum of Natural History (FMNH), and the Burke (UWBM). In total, I photographed 154 different specimens representing five different species, *Eumetopias jubatus* (Stellar Sea Lion), *Zalophus californianus* (California Sea Lion), *Phoca vitulina* (Harbor Seal), *Erignathus barbatus* (bearded seal) and *Odobenus rosmarus* (the walrus). Broken down, I used 42 specimens from *E. jubatus*, 49 specimens from *Z. californianus*, 28 specimens from *P. vitulina*, 21 specimens for *E. barbatus* and 20 specimens from *O. rosmarus*. Sea lions are represented by two out of the five species (*Z. californianus* and *E. jubatus*) and 91 different specimens. Seals are represented by two species as well (*P. vitulina* and *E. barbatus*,) but make up a smaller proportion of the total specimen count (48 total specimens). Walruses are represented by the only extant species, *O. rosmarus*, and make up the smallest proportion of the total specimen count (20 total specimens).

The seal and sea lion collection at the MNCH is substantially smaller than the collections at the other two museums. I only used three specimens, all *Z. californianus* from the MNCH. The MNCH contained a few other species but they were not the species focused on in this current study, so they were not analyzed.

Specimens from the UAM were found online at the ARCTOS database, a database that provides access to over 3 million museum records. To find the specimens, I searched for each of my selected species and selected “image” for the media type.

Searches for *Z. californianus*, *P. vitulina*, and *E. barbatus* returned no usable results (images of the underside of the skull and the side of the skull). A search for *E. jubatus* returned usable images of 23 different specimens, all with the ventral of the skull and some with lateral views of the skull.

The bulk of my specimens came from the Museum of Vertebrate Zoology at UC Berkeley. The majority of the photographs were taken over two days in December of 2016. All specimens from the species *Z. californianus*, *E. barbatus*, and *E. jubatus* were photographed during this trip using a Nikon D-200. I returned to the MVZ in December of 2017 and spent another day photographing the specimens representing *P. vitulina*. Overall, specimens from the MVZ make up about 124 out of 158 total specimens.

Later in the project, I added the walrus *Odobenus rosmarus rosmarus*, as a comparison for seals and sea lions. The specimens were collected from multiple museums. The majority, 24, came from the UAM, 10 came from the Field Museum of Natural History (FMNH), and one came from the Burke (UWBM).

Male specimens are more common in each museum collections than females for *O. rosmarus*, *E. jubatus*, and *Z. californianus*. Because of this, males make up a greater percentage of specimens for those previously mentioned three species. Male and female specimens were represented nearly evenly for *P. vitulina* and *E. barbatus* (13 females and 11 males for *P. vitulina* and 11 females and six males for *E. barbatus*). Only one of the specimens was possibly a zoo specimen (a walrus, FMNH-140831)



Figure 1: Camera Views.

A: Dorsal View of *Z. californianus* skull. B: Ventral View of *Z. californianus* skull. C: Right ventral view of *E. jubatus* skull. D: Left ventral view of *E. jubatus* skull. E: Right tooth view *Z. Californianus*. F: Left tooth of *Z. Californianus*

Camera Views

I took picture of the underside of the skull (dorsal), from both sides of the skull (lateral), from the top of the skull (ventral), and a view centered around the axis of each canine (see Fig. 1). In addition, I took pictures of the ventral and lateral sides of the jaw, though I chose to focus on only the skull for this project. I included scale bars in all photographs.

Measurements

All measurements were done on the Fiji package of the program ImageJ (Schindelin 2012; Schindelin 2015) using the images of the specimens photographed at each museum. I scaled each image using a 5-cm section of the scale bar each photograph using the “Set Scale” function. Once the scale was set, I collected a consistent set of measurements from each specimen (Carlini 2017). The scale bar had to be set prior to taking any measurements because the program is unable to apply the scale to previous measurements.



Figure 2: Measurements.

A: Tooth row measurement. B: Palate length measurement. C: Individual tooth size measurement. D: Scale bar measurement. F: Blade length measurement and width and height measurements.

I used multiple different views to take each measurement and measurement types include palate length, canine size, individual tooth size, total postcanine toothrow surface area, Postcanine toothrow length, blade length, and individual tooth width and height. I measured palate length, individual tooth size, postcanine toothrow surface area, and postcanine toothrow length using the ventral view of the skull. I took measurements pertaining to blade length and individual tooth width using the lateral views. I measured canine tooth size using the images of both the left and right canines. For the blade length, I used one lateral view with all teeth present (excluding anywhere one or more teeth have fallen out). I only used individuals with all teeth intact to

calculate total tooth surface area. Though I measured each socket (when the tooth fell out), I did not end up using the empty socket measurements in the analysis. When teeth had fallen out after death and been lost, I left the cell blank so any socket with a missing tooth was not included in any analysis.

I measured palate length and tooth row length using the “straight” tool on the Fiji toolbar. I defined palate length as the distance from the premaxillary suture to the palatine bone suture at the palatine opening and tooth row length as the distance from posterior edge of the canine to the posterior edge of the last cheek tooth. I took measurements of each individual postcanine tooth and canine tooth using the free hand selection on the Fiji toolbar. To take this measurement, I traced the maximum extent of each tooth on both the left and right side of the palate. To measure blade length, I used the linear measurement and traced the height and width of each tooth in the tooth row. I took width measurements of each tooth using the straight function. I define the width measurement as the distance from the most mesial end of a single individual tooth to the most distal end of that same tooth (see Fig. 2 for illustrations of each individual measurement). I saved all measurements in a Microsoft Excel document prior to analysis.

Statistics

I used RStudio, an open source program that provides a Graphical User Interface for the statistical program R, for all statistical work (R Core Team 2013, RStudio team 2016). RStudio reads .CSV files, so I created a new .CSV with all of the relevant measurements separate from the original Excel file. I ran linear regressions to compare tooth row length, total surface area (where it was applicable) and blade length to total

palate length. Because total surface area required that all teeth be present, I only used the individuals with a complete set of teeth for the right side of their palate. I made bar graphs comparing toothrow length, total surface area, and blade length across species to determine if those aspects were consistent across species, genera, or family (*Odobenidae*, *Phocidae*, *Otariidae*). Error bars are included and are based on standard error. I ran a Kruskal-Wallis and Dunn post-hoc test on each of those characteristics to determine which pairings are statistically significant. Only individuals with the full set of teeth in the tooth-row were included in the total surface area measurements.

I determined how variable each characteristic is by calculating the coefficients of variation for all of the collected measurements. I used the formula standard deviation/mean*100 to calculate the coefficients of variation (CV). Larger percentages suggest more variation. In addition, I took one linear measurement, the base of the tooth, and took the CVs of those measurements as well. Standard deviations and means were calculated using the core R program (R Core Team 2013).

To create the regressions, I used two different types of regression models depending on whether the data was normally distributed and/or homoscedastic. For all data normally distributed, I used an ordinary least squares regression model (OLS). OLS regressions are built into the core of R, so I ran the model using the basic R program (R Core Team 2013). For all data that were not normally distributed, I used the Theil-Sen estimator, a model that works by choosing the median of the slopes of all lines through pairs of points (Kumar 1968). This model is non-parametric and especially useful for non-normal distributions because it is less sensitive to outliers (Siegel 1982). To run the test, I used the R package “mblm” (Komsta 2013).

To determine if the means of each population are statistically different, I used the Kruskal-Wallis test by ranks. This test is a non-parametric test and does not assume that populations are normally distributed (McDonald 2015). If the Kruskal-Wallis test was significant ($p < .05$), differences between groups were calculated using Dunn's test, a non-parametric pairwise multiple comparisons procedure (Dunn 1964). The Kruskal-Wallis test is built into R (R Core Team 2013). The Dunn's test can be utilized using the package "dunn.test" (Dinno 2017). A Benjamini-Hochberg adjustment was used within the Dunn's test to limit false discovery rates and avoid type 1 errors (Benjamini 1995).


To determine if the samples are normally distributed, I created Q-Q plots and used a Shapiro-Wilk test. This test is found in the stats package of R (R Core Team 2013). To test if the data is homoscedastic, I used the Levene test. The Levene test is part of the "car" R-Package (Fox 2011). All graphs and plots were generated using the package ggplot2 (Wickham 2017). For the results of the regressions and ANOVAs that failed these tests, see the supplementary information.

To determine if the of the line was similar to 1, I subtracted 1 from the slope of the line of best fit, divided that number by the standard error and used that number in a t-table. I used the degrees of freedom from the regression test.

Results

Coefficients of Variation

Coefficients of variation vary widely with sex, family, and species (Table 1 and 2, Fig. 3 & 4). CVs range from relatively low and below ten to very high and above sixty. Few aspects have CVs of less than ten and for many aspects, the measured CVs are between fifteen and thirty (Table 1).

Species	SA Canine	SA RPC 1	SA RPC 2	SA RPC 3	SA RPC 4	SA RPC 5	SA RPC 6	Key
 F <i>Zalophus</i>	53.023765	18.537088	11.682467	22.77103	13.0191	32.30359	5.293848	< 15.5
M <i>Zalophus</i>	30.675927	14.91112	14.1922	15.5	14.47863	14.52442	14.478631	15.6-25.0
F <i>Eumetopias</i>	20.145617	24.162923	37.900419	35.416023	34.53883			25-35
M <i>Eumetopias</i>	20.010292	31.52008	36.723535	33.90844	33.72459			> 35
F <i>Phoca</i>	13.219975	13.513577	15.909142	16.125207	16.20258	17.12913		
M <i>Phoca</i>	9.428597	34.754332	24.591148	16.340859	16.11267	15.38304		
M <i>Erignauthus</i>	19.159252	28.614798	42.31464	21.304281	24.59855	24.71488		
F <i>Erignauthus</i>	28.1340182	43.3725715	43.006247	34.870343	44.70516	38.02123		
M <i>Odobenus</i>			22.010667	31.056995	19.02242	25.06057		
F <i>Odobenus</i>			65.628035	13.32512	20.95399	13.08378		



Species	UL Canine	SA LPC 1	UL SA 2	UL SA 3	UL SA 4	UL SA 5	UL SA 6
 F <i>Zalophus</i>	39.371469	23.334435	24.029232	21.722332	7.32879	20.1869	21.551834
M <i>Zalophus</i>	38.735627	16.317738	12.468321	14.411853	16.14338	18.97259	10.515018
F <i>Eumetopias</i>	9.677108	35.435888	25.920272	35.981913	33.47438		
M <i>Eumetopias</i>	23.707672	31.158433	43.115726	34.97941	39.55526		
F <i>Phoca</i>	10.614623	11.231095	12.854769	16.863218	15.91051	14.69382	
M <i>Phoca</i>	11.170741	31.450262	23.221645	19.449493	14.13156	9.734673	
M <i>Erignauthus</i>	19.627392	27.068409	36.468906	18.396601	30.54478	28.94985	
F <i>Erignauthus</i>	27.0859768	47.9107228	45.188414	38.496422	16.87649	29.90635	
M <i>Odobenus</i>			23.723849	23.285264	21.81226	23.00413	
F <i>Odobenus</i>			40.466951	29.910794	23.6124	21.70762	

Table 1: Table displaying coefficients of variation for canine and tooth surface area in each species for surface areas for right (upper) and left (lower) sides of the palate.

The pictures to the left side represent family associations (i.e. Otariidae). Color-coded based on size of CV. Abbreviations: SA= surface area, RPC= Right Post Canine, LPC= left post canine. Post canine number dependent on placement relative to canine (post canine 1 directly posterior to canine).



Species	R Toothrow	L Toothrow	Blade Length	W PC 1	W PC 2	W PC 3	W PC 4	W PC 5	W PC 6
F <i>Zalophus</i>	12.358068	8.485251	15.549773	4.677566	20.104842	12.48334	17.10203	15.549106	1.57954
M <i>Zalophus</i>	14.669166	13.335781	10.736284	15.059735	11.653265	13.0674	12.78235	17.339174	25.0301
F <i>Eumetopias</i>	22.912063	23.211221	14.03582	20.901876	17.719021	18.98519	13.28274	25.540172	
M <i>Eumetopias</i>	19.79651	18.714704	7.600121	12.694254	14.174678	9.723899	8.552786	14.103887	
F <i>Phoca</i>	8.088115	9.117601	14.966578	14.963067	21.016158	14.97341	11.36072	15.080492	
M <i>Phoca</i>	10.714065	12.346857	12.126158	14.836476	9.960866	12.62142	9.316234	9.71558	
M <i>Erignathus</i>	10.13134	9.142133	10.682373	16.808952	21.319086	13.64321	19.30467	13.579956	
F <i>Erignathus</i>	3.7852927	4.4611352	10.3693901	19.975424	16.007783	16.10354	18.67729	14.840622	
M <i>Odobenus</i>	8.708491	7.372068							
F <i>Odobenus</i>	9.477371	8.517199							

Table 2: Table displaying coefficients of variation for each species for tooth-row length, blade length, and right tooth width.

The pictures to the left side represent family associations (i.e. Otariidae). Color-coded based on size of CV (see table 1). Abbreviations: W= width, PC= Post Canine. Post canine number dependent on placement relative to canine (post canine 1 directly posterior to canine).

SA Right Canine	SA Postcanine 1	SA Postcanine 2	SA Postcanine 3	SA Postcanine 4	SA Postcanine 5	SA Postcanine 6		
24.2246804	26.17331119	31.39584996	24.06182978	23.73565255	22.5275789	9.8862395		
SA Canine	SA Postcanine 1	SA Postcanine 2	SA Postcanine 3	SA Postcanine 4	SA Postcanine 5	SA Postcanine 6		
22.4988261	27.98837285	28.74580854	25.34972996	21.93898141	20.89449089	16.033426		
R Toothrow Len	L Toothrow Len	Blade Length	W Postcanine 1	W Postcanine 2	W Postcanine 3	W Postcanine 4	W Postcanine 5	W Postcanine 6
12.06404817	11.47039502	12.00831214	14.98966876	16.49446243	13.9501773	13.79735195	15.71862356	13.304815

Table 3: Table displaying average coefficients of variation for each aspect.

Color-coded based on the size of the CV (see table 1). Top row: right side. Middle row: Left side. Post canine number dependent on placement relative to canine (post canine 1 directly posterior to canine).

Though CVs vary widely between families, species, and even between sexes, CVs differ in their relative size depending on the aspect. Total surface area measurements have relatively high CVs with very few CVs below ten (Table 1, Fig. 3 and 4). There is little pattern in the variation within the tooth row for surface area, with some species having mostly similar CVs across the entire postcanine toothrow (*Z. californianus*, *P. vitulina*) and others having inconsistent CVs across the toothrow (*E. jubatus*, *E. barbatus*, *O. rosmarus*) (Table 1). Sex also influences the measured CVs in some species but not consistently across species or within genera. For example, female *O.*

rosmarus have a highly variable second right postcanine compared to the males (65 versus 22) and male *P. vitulina* have a highly variable first postcanine compared to females (34 vs. 13) (see Table 1).

CVs for linear measurements (blade length, toothrow lengths, and tooth widths) were, in general, lower than CVs for postcanine surface areas and canine surface areas (Tables 1 and 2, Fig. 1 & 2). Excluding *E. jubatus*, variation for toothrow lengths and blade lengths was low, with CVs consistently at 15.5 or below. This trend of low CVs for the more linear measurements (compared to the surface area measurements) is relatively constant across species and the average postcanine CV for the linear measurements are, in general, lower than surface area measurements (Table 3).

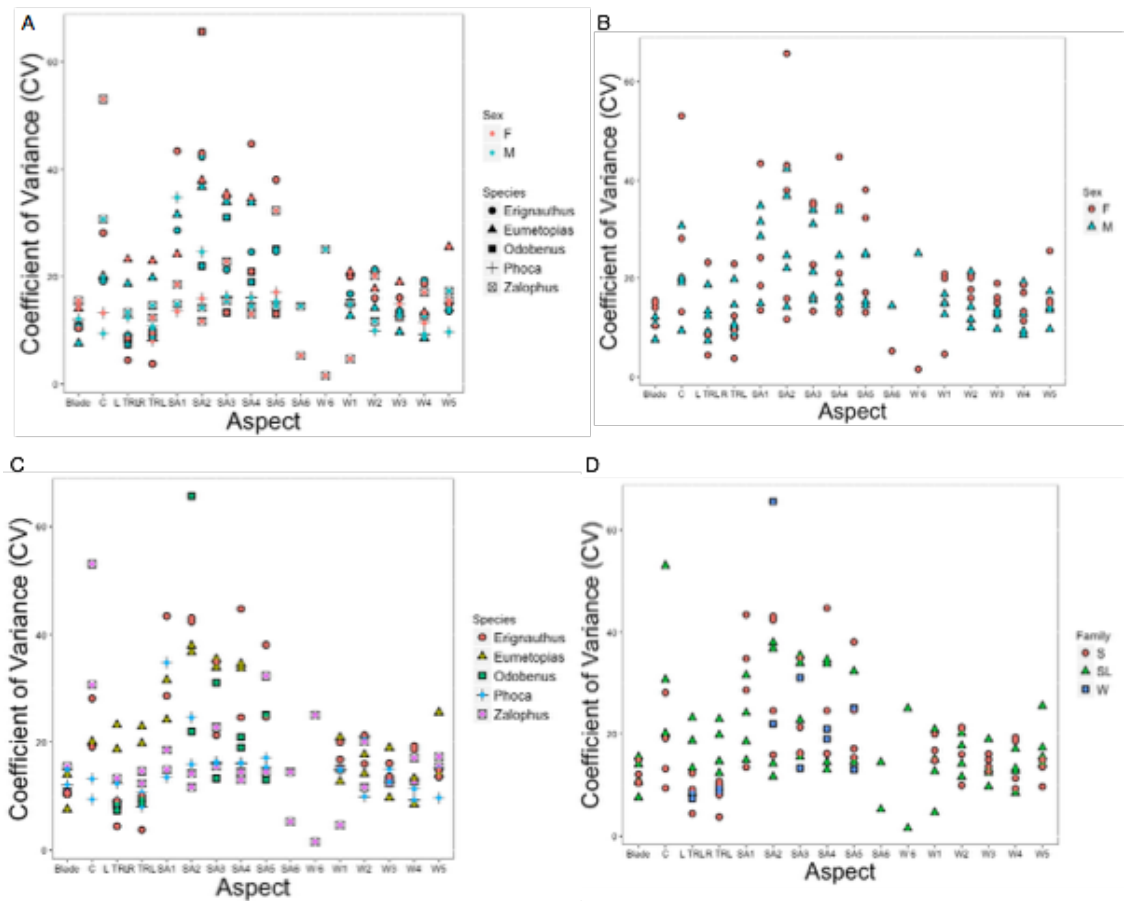


Figure 3: Plots of coefficients of variation and specific aspect for right surface areas, right tooth widths, blade length, and left and right tooth length.

A: Plot of CV with sex and species marked. B: plot of CV with sex marked, C: plot of CV with species only marked. D: Plot of CV with family marked.

Some patterns emerge in between-species comparisons (Fig. 3c & Fig. 4c). *Zalophus californianus* shows the some of the lowest variation for a number of different aspects, including right and left postcanines 2, 3, and 4 and as a species has some of the lowest calculated CVs overall (see Table 1 & Table 2, Figs 3c & 4c). However, variation is high for both canines (see table 1, figure 3c). *Phoca vitulina* has consistently similar

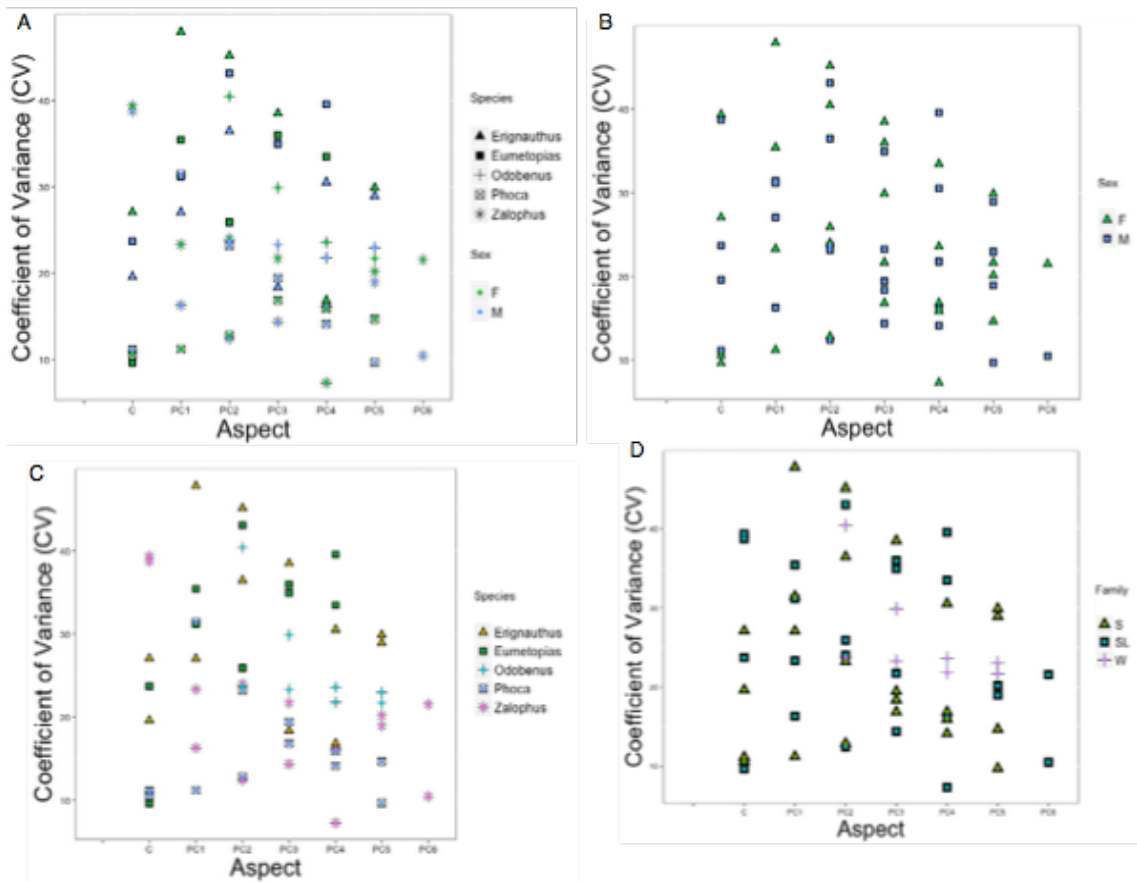


Figure 4: Plots of coefficients of variation for right surface areas, right tooth widths, blade length, and left and right tooth length. A: Plot of CV with sex and species marked. B: plot of CV with sex marked, C: plot of CV with species only marked. D: Plot of CV with family marked.

variation, and has either the lowest or the second lowest CV for both left and right postcanine 2, 4, and 5 (surface area and postcanine width) (see Table 1 & Table 2, Fig 3c & 4c). Comparatively, *E. barbatus* and *E. jubatus* have the highest CVs and *O. rosemarus* has intermediate CVs (see Table 1 & Table 2, Figures 3c & 4c). There is, however, no one species with consistently the lowest or highest CV. There appears to be little pattern in levels of variation in sex as well as species (table 1b and 2b).

Across species, there is little evidence that in general, one sex has consistently lower CVs than the other sex. Similarly, in the species studied, there is little evidence

that a specific family (*Otariidae*, *Odobenus* or *Phoca*) has lower CVs than another family (Table 1D and 2D). The value of the specific CV depends primarily on the aspect being measured and the species. There is little evidence from my calculated values that one specific species or sex or family has consistently lower or higher CV values than the other species or sex or families. The only observable pattern that occurs between species, sexes, and families is that toothrow lengths, postcanine width measurements, and blade length measurements have consistently lower CVs than surface area measurements, with most of the lowest values for CVs calculated for those three aspects.

Relationship to Palate Length

The length of the right and left toothrows both appear to be associated with total length of the palate (Fig. 3&4). For transformed values, we would expect a slope of one for any line of best fit if the two values are isometric (that is, if they are scaling in a way that is proportionate to each other). The line of best fit, calculated using the Theil-Sen repeated median linear model, has a slope of 1.0055, a slope that is not significantly different from 1 ($P > .05$), suggesting that right toothrow length is scaling isometrically with palate length. The calculated line of best fit for the left side of the toothrow using the Theil-Sen repeated linear model has a slope of 1.06 and a p-value that is also not statistically different from 1 ($p < .05$). Toothrow length for both the left and right jaw are increasing isometrically with palate size on a species level scale (Fig. 5a and 6a) and the largest species also have the longest tooth rows (i.e., *O. rosmarus* and *E. jubatus* have some of the largest tooth rows whereas *P. vitulina* has some of the smallest).

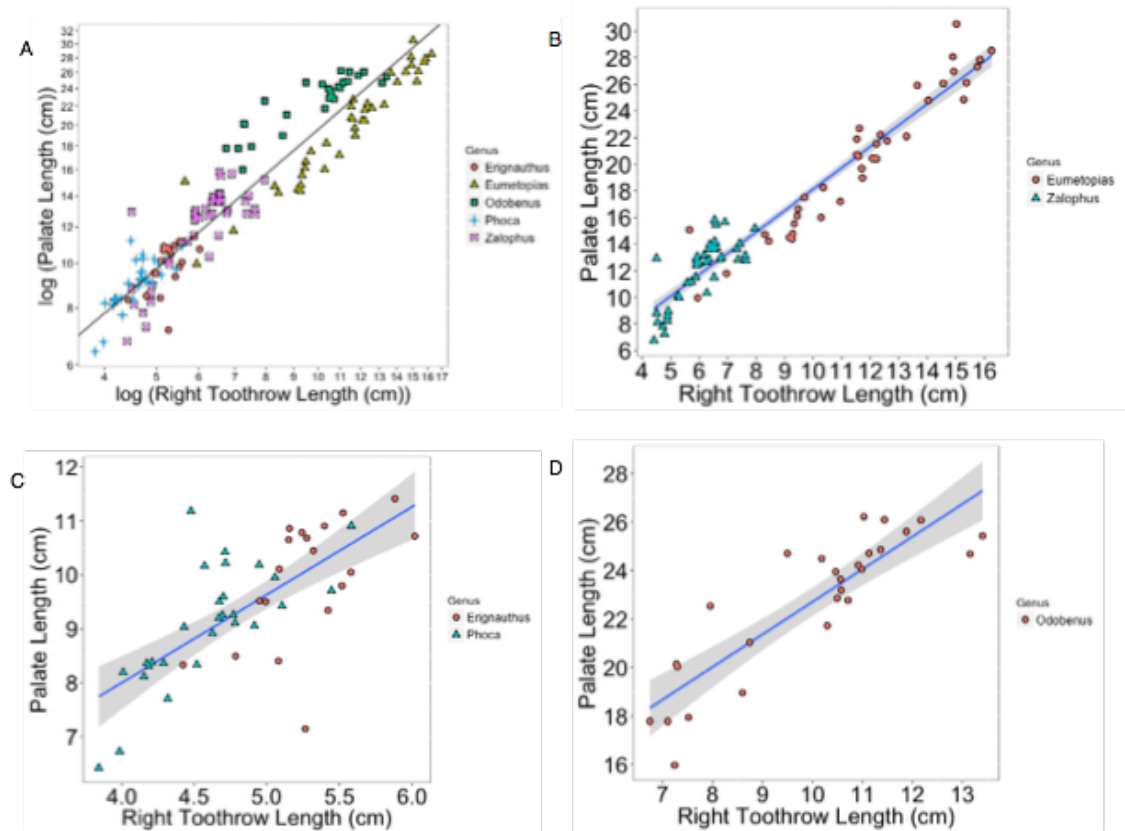


Figure 5: Relationship of palate length to right tooththrow length.

A: All species included, Theil-Sen repeated linear model used. Slope = 1.005, P-value = 2×10^{-16} . The slope of the line is statistically no different than one (calculated p-value for the difference between the slope and one is greater than .05). B-D: least squares regression on right tooththrow length and palate length for each family. B: Otariidae. Slope = 1.60324, $R^2 = .9243$, p-value = 2×10^{-16} . C: Phocidae: Slope = 1.6236, $R^2 = .4832$, p-value = 3.56×10^{-8} . D: Odobenidae: Slope = 1.3413, $R^2 = .752$, p-value = 2.95×10^{-9} .

Similar positive relationships are found between the untransformed tooththrow lengths and palate lengths of species within each family (Fig 5 B-D, Fig 6 B-D). Palate length is positively correlated with both left and right tooththrow length across all five species and within individual families and species (Fig. 5 A-D and Fig. 6 A-D). Within families, tooththrow length appears to be tightly correlated with palate length, especially

in Otariidae (Fig 5B and Fig.6B). Toothrow length appears to be least correlated with body size in Phocidae, especially in the species *P. vitulina* (Fig. 5C and Fig. 6C).

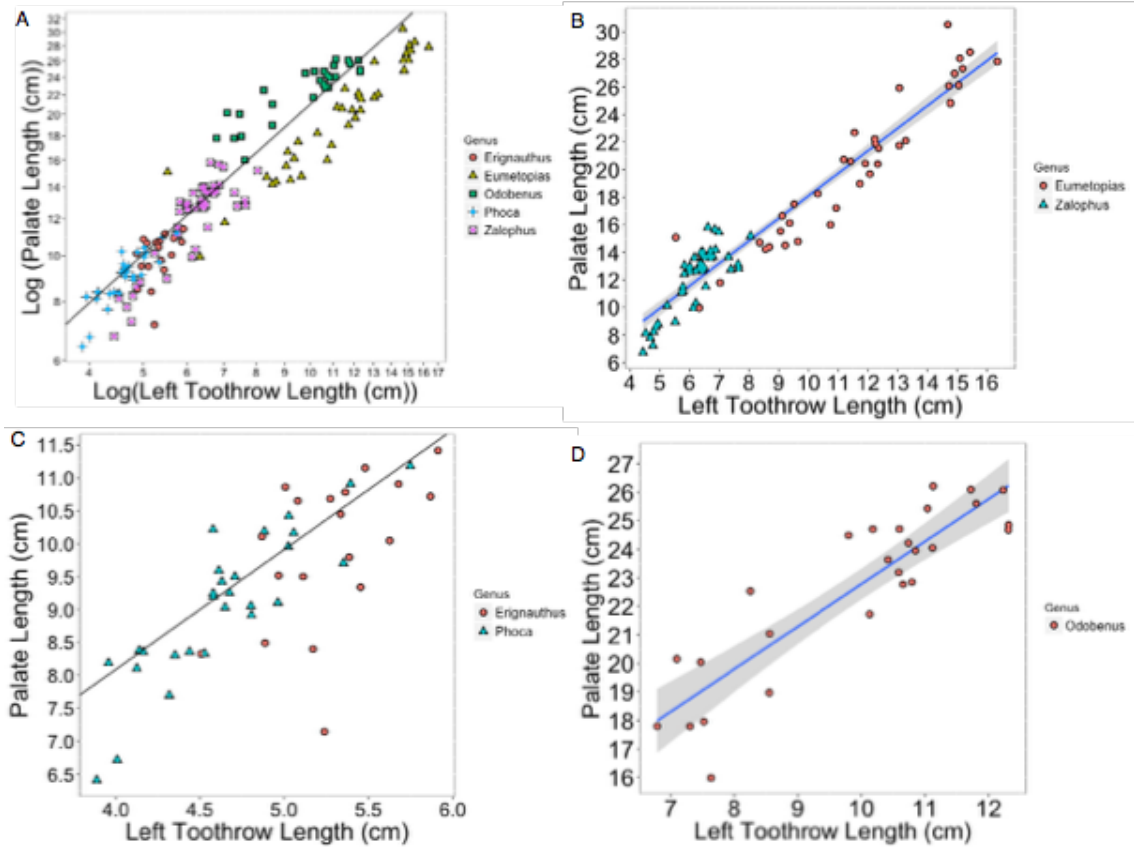


Figure 6: Relationship of palate length to left toothrow length.

Figure A: All species included, Theil-Sen repeated linear model used. Slope = 1.0606, P-value = $2e^{-16}$. The slope of the line is statistically no different than 1 (calculated p-value for the difference between the slope and one is greater than .05). **B-D:** least squares regression on left toothrow length and palate length for each family. **B:** *Otariidae*. Slope = 1.63285, $R^2 = .9209$, p-value = $2e^{-16}$. **C:** *Phocidae*: Slope = .9501, $R^2 = .57$, p-value = 5.275×10^{-10} . **D:** *Odobenidae*: Slope = 1.4915, $R^2 = .7845$, p-value = 5.013×10^{-10} .

Blade length, when log transformed, is also positively correlated with palate length (see Fig. 7a). Species with longer palates, for example, *O. rosmarus* have longer blade lengths compared to animals with shorter palate lengths. However, unlike the slope of

the line of best fit between palate length and left and right tooththrow length, the slope for the line of best fit for palate length and blade length is not significantly indistinguishable from one (slope of line of best fit calculated by a linear regression = .6478, p-value \ll .05).

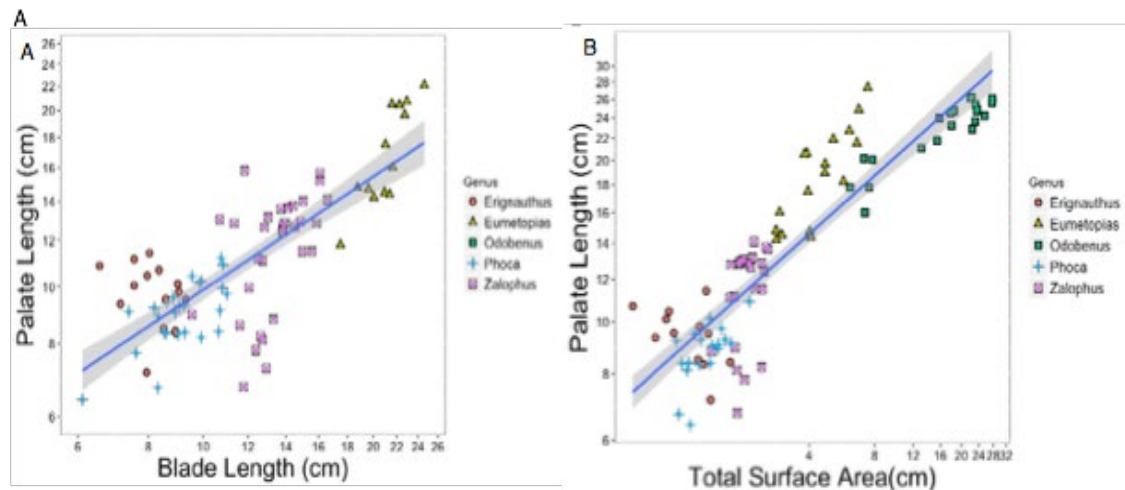


Figure 7: Relationship of logged palate length to logged blade length and logged total surface area. **A:** Relationship of logged palate length to logged blade length. All species. Slope = .64778, $R^2 = .6526$, p-value = $2.2e^{-16}$. **B:** Relationship of logged palate length to logged total surface area. All species. Slope = .34555, $R^2 = .7706$, p-value = $2.2e^{-16}$.

Similarly, total surface area and palate length of each specimen is also positively correlated. However, like blade length, a linear regression comparing logged values for total surface area and palate length does not generate a line of best fit with a slope of one (see Fig. 7b). Instead, the slope returned by this particular regression is .35720, a slope that is significantly different from 1 ($p \ll .05$). The slope of this linear regression is positive, and the smallest species (or individuals) have a smaller total surface area. However, the slope of the line of best fit is statistically different from one, suggesting that palate length and total surface area are not scaling isometrically. Instead, both blade

length and total surface area have allometric scaling. Though blade length and total tooth surface area are increasing with palate length, the changes are not proportional to the changes in body length.

Relationships In Mean Sizes Between Species

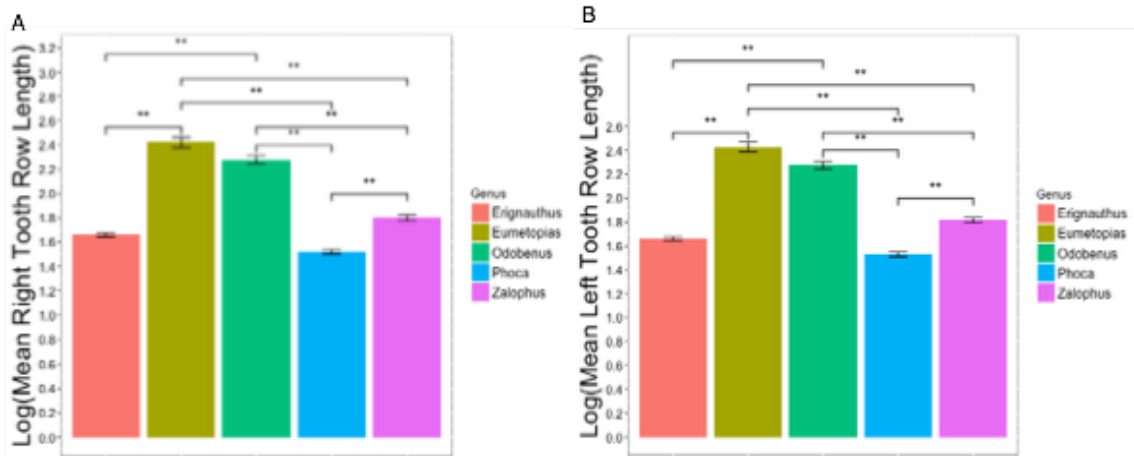


Figure 8: Comparison of right and left toothrows for each species.

A: Comparison of right roothrow length. pairings that are significantly different are: *E. jubatus* x *E. barbatus* ($p < .0001$), *O. rosmarus* x *E. barbatus* ($p < .0001$), *E. jubatus* x *P. vitulina* ($p < .0001$), *O. rosmarus* x *P. vitulina* ($p < .0001$), *E. jubatus* x *Z. californianus* ($p < .0001$), *O. rosmarus* x *Z. californianus* ($p < .0001$), *Z. californianus* x *P. vitulina* ($p = .0001$). **B:** pairings that are significantly different are: *E. jubatus* x *E. barbatus* ($p < .0001$), *O. rosmarus* x *E. barbatus* ($p < .0001$), *E. jubatus* x *P. vitulina* ($p < .0001$), *O. rosmarus* x *P. vitulina* ($p < .0001$), *E. jubatus* x *Z. californianus* ($p < .0001$), *O. rosmarus* x *Z. californianus* ($p < .0001$), *Z. californianus* x *P. vitulina* ($p < .0001$). Error bars are based on standard error.

The mean size of tooth-row lengths differs depending on the species. The larger species (*E. jubatus* and *O. rosmarus*) have significantly larger left and right toothrows than other species (see Fig. 8). The smallest species, *P. vitulina*, has a left and right mean toothrow that is smaller than all other species except *E. barbatus* for both the left and

right side of the mouth (Fig. 8). Both left and right tooththrows in *E. barbatus* are significantly smaller than *E. jubatus* and *O. rosmarus*, but similar in size to *Z. californianus* and *P. vitulina*.

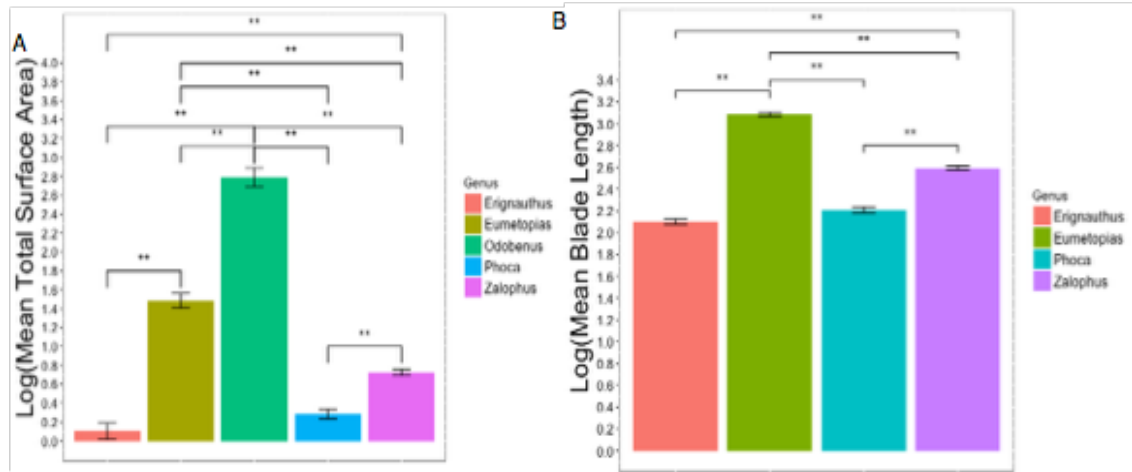


Figure 9: Comparison of total surface area and blade length for each species.

A: Comparison for total surface area. significantly different pairings include *E. jubatus* x *E. barbatus* ($p < .0001$), *O. rosmarus* x *E. barbatus* ($p < .0001$). *E. jubatus* x *P. vitulina* ($p < .0001$), *E. jubatus* x *O. rosmarus* ($p = .0216$), *O. rosmarus* x *P. vitulina* ($p < .0001$), *E. jubatus* x *Z. californianus* ($p = .0216$), *O. rosmarus* x *Z. californianus* ($p < .0001$), *Z. californianus* x *P. vitulina* ($p = .0157$), *Z. californianus* x *E. barbatus* ($p = .0061$). **B.** Comparison for mean blade length. Significantly different pairing include: *E. jubatus* x *E. barbatus* ($p < .0001$), *E. jubatus* x *P. vitulina* ($p < .0001$), *Z. californianus* x *E. barbatus* ($p < .0001$), *E. jubatus* x *Z. californianus* ($p = .0028$), *Z. californianus* x *P. vitulina* ($p < .0001$). Error bars are based on standard error.

For blade length, two of the species, *P. vitulina* and *E. barbatus* have the smallest mean blade lengths (Fig. 9). Blade length for both species are statistically similar to each other, but statistically different than the other two species (Fig. 9). Mean blade length in both *Z. californianus* and *E. jubatus* is statistically different than all other studied species (see Fig. 9). Blade length was not calculated for *O. rosmarus* because the teeth in that species are flattened and lack individual cusps to form any blade-like structures.

Total surface area is much more variable in size than either tooth-row length or blade length. All pairings for total surface area except for *E. barbatus* & *P. vitulina* are significantly different. The largest species, *O. rosmarus* has the largest total surface area. The smallest species, *E. barbatus* and *P. vitulina*, have the smallest total surface area.

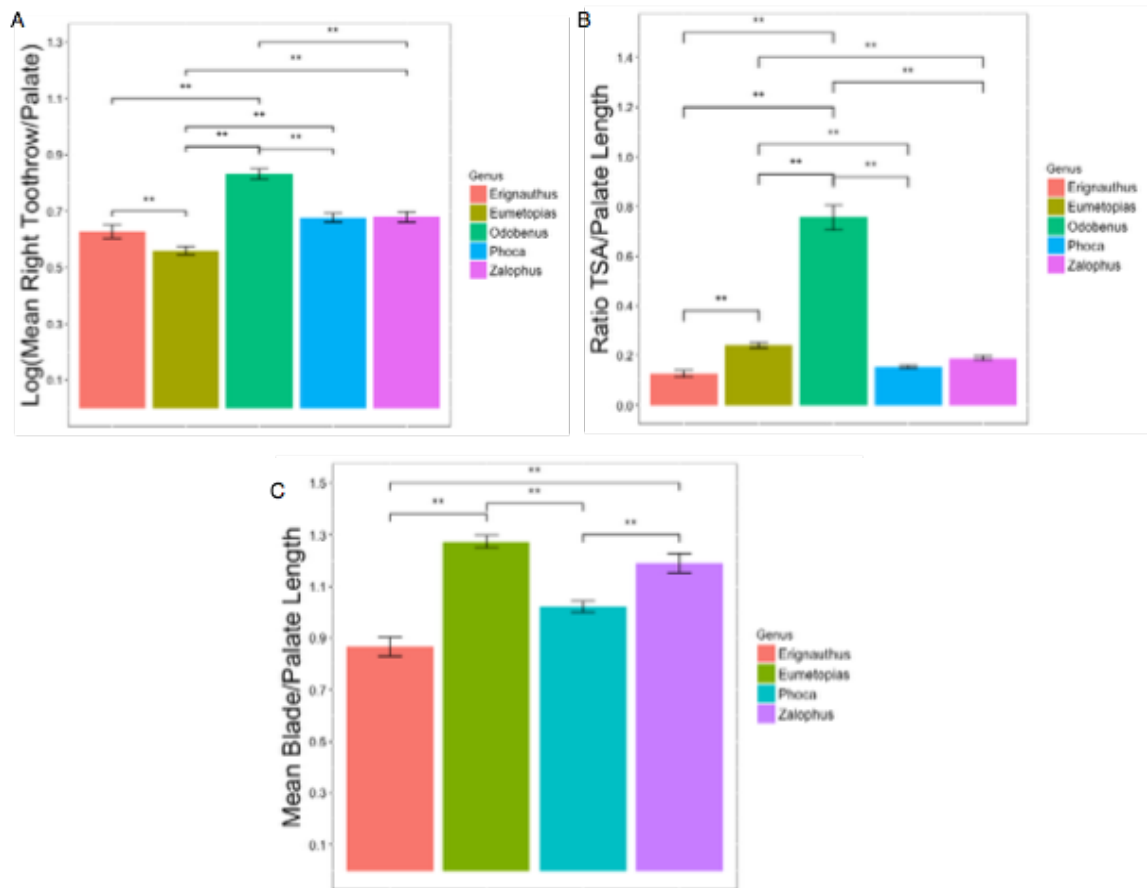


Figure 10: Comparison of mean right tooththrow length, blade length, and total surface area when each of those aspects is divided by palate size. **A:** Comparison of right tooththrow length. Pairings that are significantly different are: *E. jubatus* x *E. barbatus* ($p < .0222$), *O. rosmarus* x *E. barbatus* ($p < .0001$), *O. rosmarus* x *E. barbarous* ($p < .001$) *E. jubatus* x *P. vitulina* ($p < .0001$), *O. rosmarus* x *P. vitulina* ($p = .0002$), *E. jubatus* x *Z. californianus* ($p < .0001$), *O. rosmarus* x *Z. californianus* ($p < .0001$), *Z. californianus*). **B:** Comparison for total surface area. significantly different pairings include *E. jubatus* x *E. barbatus* ($p < .0001$), *O. rosmarus* x *E. barbatus* ($p < .0001$). *E. jubatus* x *O. rosmarus* ($p = .0074$), *E. jubatus* x *P. vitulina* ($p = .0007$), *O. rosmarus* x *P. vitulina* ($p < .0001$), *E. jubatus* x *Z. californianus* ($p = .0483$), *O. rosmarus* x *Z. californianus* ($p < .0001$), *Z. californianus* x *E. barbatus* ($p = .0230$). **C.** Comparison for mean blade length. Significantly different pairing include: *E. jubatus* x *E. barbatus* ($p < .0001$), *E. jubatus* x *P. vitulina* ($p < .0001$), *Z. californianus* x *E. barbatus* ($p < .0001$), *Z. californianus* x *P. vitulina* ($p < .042$). Error bars are based on standard error.

Normalizing each aspect (tooththrow length, blade length, and total surface area) by dividing each measurement by the corresponding palate length measurement maintains

variation is mean size of each of those aspects across species (Fig. 10). Many of the differences are the same. For toothrow length, dividing toothrow length by palate length created a new statistically significant difference in mean between *E. jubatus* and *O. rosmarus* and eliminated the significant difference in means between *Z. californianus* and *P. vitulina*. (Fig. 10A) Similarly, the significantly different relationships in mean blade length when blade length is normalized is nearly identical to the non-normalized blade length (Fig. 10B). Normalizing eliminated a distinction between *Z. californianus* and *P. vitulina* but all the other relationships stayed the same. Finally, normalizing total surface area eliminated the distinction in mean total surface area between *E. jubatus* and *Z. californianus* only (Fig 10C). All other relationships remained the same.

Discussion

Species	Sample Aspect	Sample CV	Sample Aspect 2	Sample CV 2	Sample Aspect	Sample CV	Paper
<i>Canis lupus</i>	P ² length	5.94	P ¹ Li (measure of length)	3.68	Tooth Row Length	3.16	Dayan 2002
<i>Felis silvestris</i>	P ² length	25.19	P ¹ Li (measure of length)	5.78	Tooth Row Length	3.87	Dayan 2002
<i>Ursus americanus</i> *	M ² Breadth	5.4	M ¹ breadth	5.5			Miller 2009
<i>Ursus spelaeus</i>	M ¹ Length (metacone)	6.18	M ² Length (metacone)	9.27			Baryshnikov 2003
<i>Martes Martes</i> **	Length Lower Canine	4	Length lower m1	3.2	Tooth Row Length	2.7	Reig 1992
<i>Martes Foina</i> ***	Length Lower Canine	3.9	Length lower m2	2.6	Tooth Row Length	2.5	Reig 1993
*Taken from the Newfoundland Population							
**Taken from the Cantabrian mountain population							
***Taken from the Pyrenees population							

Table 4: Table with some sample characteristics of different species and their corresponding CVs

The calculated CVs for pinnipeds vary depending on the characteristic (i.e. toothrow length or blade length) and species tested and CVs range from over sixty-five to under ten (Table 1). Average calculated CVs for all pinnipeds are lower, but still range from over twenty-five to over ten (Table 4). Linear measurements tend to be lower than measurements looking at the surface area of an individual tooth and total blade lengths and toothrow lengths tend to have the lowest CVs out of all different aspects.

Pinnipeds have, in general, higher CVs than other species of mammals. Most examined species of non-pinniped carnivorans tend to have CVs under 10%, though some species such as *F. silvestris* may have some outliers over 10%, such as the 25.19 value for the length of the 2nd upper premolar (see Tables 1, 2, and 4 for some comparison CVs). The CVs I calculated for pinnipeds are rarely under 10% for any of the examined species. The lowest CVs were for linear measures (left and right toothrow lengths and post-canine tooth lengths), however most averages are still above 10.0 (ranges from 12-15). CVs for some species and sexes, however, have similar values to those CVs found in terrestrial carnivores (the width of PC1 in female *Z. californianus*, for example, has a CV of 4.68). In general, however, CVs are higher in species of

pinniped than CVs are in terrestrial carnivores like bears, cats, and mustelids. They are somewhat comparable for CVs determined for less precisely occluding teeth in terrestrial mammals (for example, the second upper premolar in *F. silvestris*). This suggests that pinniped teeth are, in general, more variable than teeth of other terrestrial, including the terrestrial groups they are most closely related to (bears and weasels). However, like in *F. silvestris* and *C. lupus*, CVs for tooth-row lengths in pinnipeds are generally some of the lowest.

Increased variation in pinniped teeth may be due to a lack of balancing selection, because their teeth are not used for mastication and therefore do not need to occlude precisely. The typically low variation found in carnassials in terrestrial species is likely the result of balancing selection, because the teeth have a specialized crown structure and need to occlude very precisely to properly masticate food (Miller 2009; Gingerich 1979; Meiri 2005). Because of the feeding mechanics in these five species (either pierce feeding or suction feeding) the tooth need only be present for catching and holding food and the size of the tooth is less important than the fact that the tooth is present at all (Adam 2002). Although this would not explain the isometric relationship between the size of the tooth row and the size of the palate, it may explain why each individual tooth is variable in size. Therefore, is likely that the relatively simple, peg-like teeth in pinnipeds are not under the same high selective pressures as carnassials for hypercarnivory. This may be reflected in the variation data: the lowest CVs are found in traits that are useful for catching and holding fish- the overall length of the toothrow, the total length of tooth blade for catching fish (blade length) and the length of each individual tooth.

However, the high variation in the size of pinniped teeth may be a consequence of recent, quick increase in body size. Marine mammals like cetaceans, sirenians and pinnipeds, face different stress than terrestrial mammals (Churchill 2015a). Living in water increases the amount of energy dedicated to thermoregulation, constraining the minimum body size in pinnipeds far above the minimum body size in terrestrial mammals. The fossil record for pinnipeds is patchy; however the earliest diverging (and now extinct) lineage of stem pinnipeds belong to the Pinnipedimorpha are relatively small (Berta 2018). One species, *Enaliarctos measli*, were relatively small, between 1.4 and 1.5 meters, about the size of a small male harbor seal, suggesting that early pinnipeds started out relatively small and grew over time to the sizes they are today (Berta 2018).

The earliest known and described otariid, *Pithanotaria starri* (Deméré 2003) from the Hemphillian North American Land Mammal Age, is one of the smallest known otarriids at about 126 cm (Churchill 2015b) and older, undescribed otariid taxa are likely similarly sized (Churchill 2015b). An increase in size occurred relatively early in the Otariidae lineage (Churchill 2015b). Similarly, early species in Odobenidae also relatively small at 195 cm, drastically smaller than extant walruses and smaller than almost all fossil walruses (Churchill 2015b). This species exhibited a rapid increase in size during the Miocene (Churchill 2015b). The fossil record for Phocidae, in comparison to Otariidae and Odobenidae is especially poor, making size reconstruction difficult. Within the clade, Monachines appeared to increase in body size with time and Phocinae appeared to decrease with time, though the exact timing for both the increase and the decrease is unknown (Churchill 2015b). It is possible that some of the variation

in teeth size may be driven by a rapid change in body size, especially in the case of species in Otariidae and Odobenidae, since both underwent fairly rapid increases in body size.

Variation within a few of the different aspects measured, blade length, toothrow lengths, and total surface area, may be related to the overall body size of the organisms. For both logged tooth row lengths versus palate length, a Theil-Sen estimator produces a line with a slope that is not statistically different from one. This slope of one, because both variables are logged, suggests that tooth row length is scaling with overall body size (isometric scaling). When one increases, the other increases proportionately. Those species with larger palate lengths, at least in the species I selected, have larger toothrow lengths. For each individual family, linear regressions of toothrow lengths versus palate length produce lines-of-best fit that have positive slopes, suggesting that tooth-row length is increasing both within individual families and individual species. In pinnipeds, previous research has determined that length of the animal's palate is an accurate estimation of body length within the family Otariidae (Churchill 2014). Together, the evidence presented suggests that the size of the toothrow is related to the size of the animal. Larger species, and larger animals within species, have larger toothrow lengths.

Logged blade length is also positively correlated with logged palate length (slope of the predicted line-of-best fit = .6478, see Fig. 7a). However, that slope is not statistically indistinguishable from one ($P\text{-value} > .05$), suggesting that although palate size and blade length are positively correlated, blade length is not increasing as much as expected in relation to body size. Instead of isometric scaling, blade length and palate length have an allometric relationship. Because the slope is below one, the allometric

relationship is negative and blade length does not increase as much as expected with larger palates. Blade length is also correlated with larger sized species and larger sized individuals. We would expect that bigger species and bigger individual within in those species have larger blade lengths.

Finally, the logged values for total tooth surface area is positively correlated with logged values for palate length (Fig. 7b). Like with blade length, total tooth surface area is scaling with body size so both the relationships are allometric. Though total tooth surface area does increase as palate length (and therefore body size) increases, it does not increase as greatly as we would expect in relation to body size. Larger animals and species do tend to have larger total surface areas, however the change as body size increase is not as large as one would expect if the two aspects were scaling isometrically. Some of the variation, however, for all three aspects (toothrow length, blade length, and surface area) is related to how large the animal is.

The regressions presented above suggest that a certain blade length, tooth-row length, or total surface area is not conserved across species (see Fig. 5a, 6a, 7a & 7b). Further, the mean size of each of those aspects vary depending on the species I examined (Fig. 9 and 10). For all three of those different aspects, toothrow length, blade length, and total surface area, the largest species studied (*O. rosmarus* and *E. jubatus*) had the largest of each and the smallest species (the phocids) had the smallest.

For these species, despite having relatively similar diets, there does not appear to be an ideal toothrow length, blade length, or total surface area for catching and holding prey. It is true that diets do differ. *O. rosmarus*, for example, has a unique way of feeding among pinnipeds. Instead of using its teeth for pierce feeding, it uses them to

position and hold clams and other hard-shelled invertebrates. It then uses suction to remove those organisms from their shells. However, though perhaps *O. rosmarus* has a unique feeding technique, the mean sizes of those aspects in species that do share similar feeding types still differ. *P. vitulina*, *Z. californianus* and *E. jubatus* all utilize pierce feeding, but still differ in the mean size for all three aspects. In contrast, *P. vitulina* and *E. barbatus* use different feeding methods (pierce feeding for *P. vitulina* and suction feeding for *E. barbatus*) but have similar mean size for all three of those aspects. For these five species, overall body size appears to contribute to the overall size of the tooth-row length, blade length, and total surface area.

Normalizing each of those three characteristics by body size by dividing each by palate length does not eliminate the differences in means across species (Fig. 10). This suggests that, even taking body size into account, there is no ideal toothrow length, blade length, or total surface area.

Future Directions

To strengthen this project, I think it would be useful to add some more specimens of each different species. By adding more specimens, the CVs may lower to similar levels as the CVs published in other papers. In addition, I think it would be useful to add a few more species to my analysis. It would be useful to add one more species in both Otariidae and in Phocidae. For Phocidae, I selected two relatively small seals. It might be useful to add in a larger bodied phocid, such as the leopard seal (*Hydruga leptonyx*). In addition, to really determine if crown complexity affects how variable teeth are, a pinniped with teeth that are more functional, such as the crabeater seal (*Lobodon carcinophagus*), should be added

In addition, I think variation should be measured in at least one species of ursid (a close relative) and one species of felid or canid. In addition, it might be useful to look at variation in another secondarily aquatic mammal, such as the a dolphin because they are ecologically similar. By making my own measurements on these types of carnivores, I can ensure that differences in CVs I determine are due to differences across species and not differences in measuring techniques between researchers (for example, the use of calipers or the use of ImageJ). I think it may be useful to look at different measures of variation as well, such as variance-to-mean ration.

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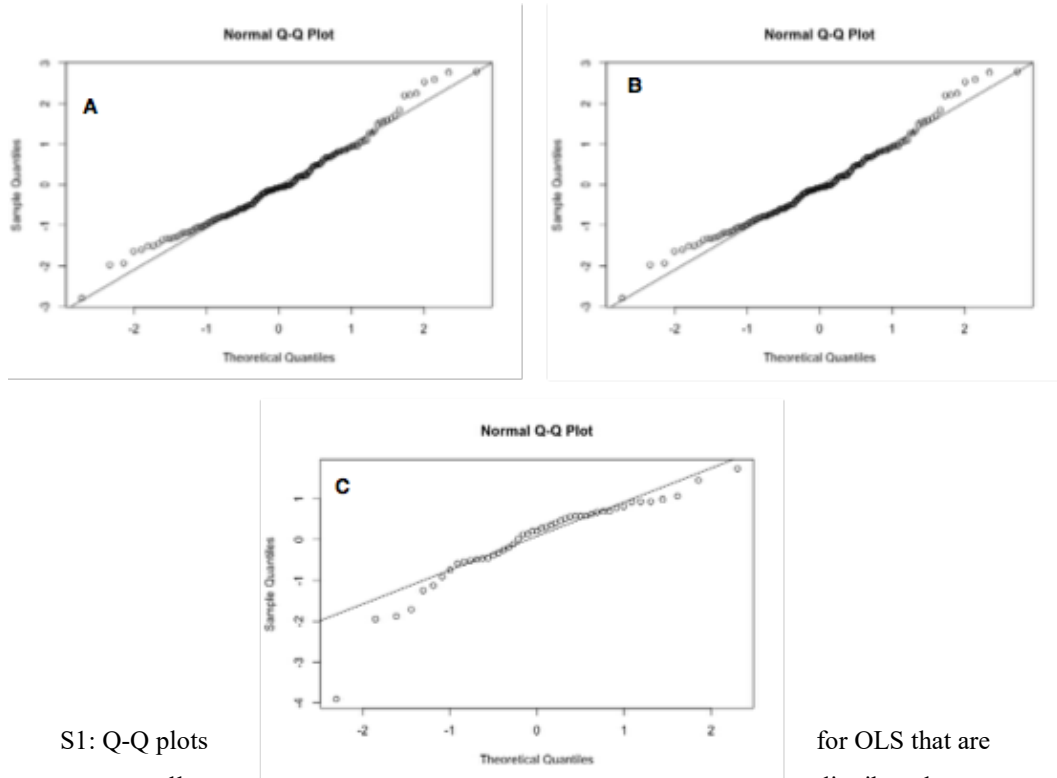
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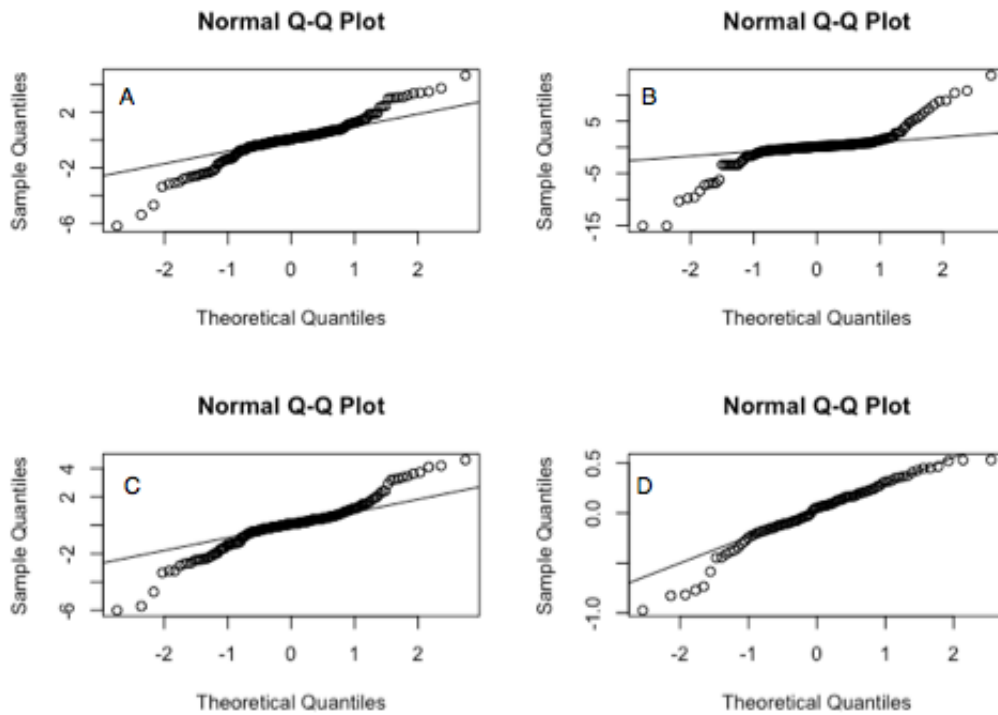
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Supplementary Information

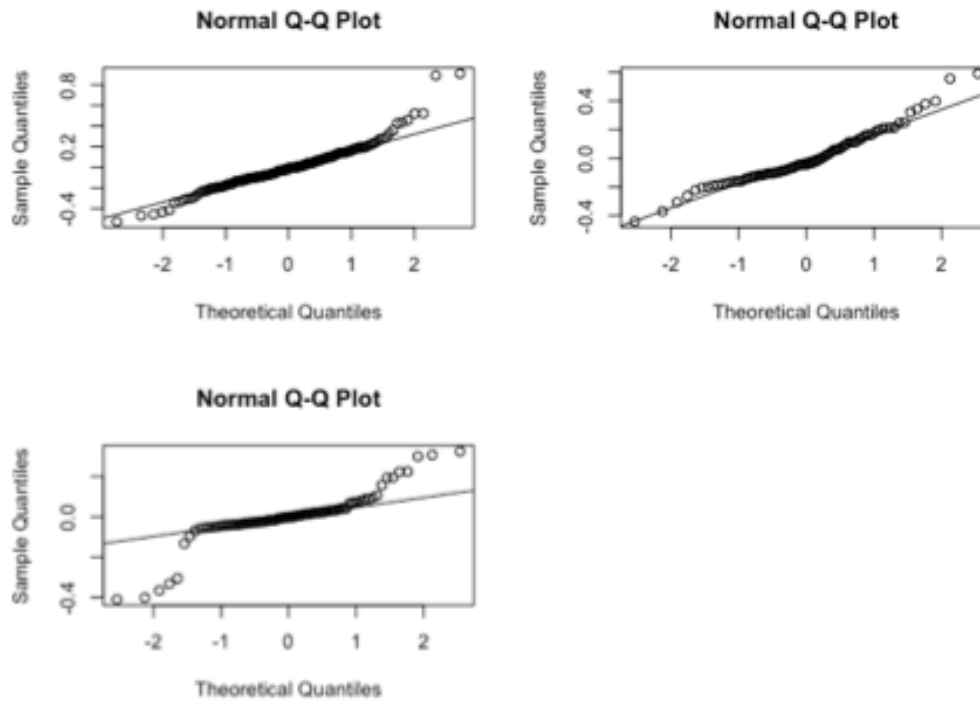


A: Residuals for the OLS regression on right toothrow length and palate length. Results of Shapiro-Wilk normality test: $p=.03584$. B: Residuals for the OLS regression on left toothrow length and palate length. Results of Shapiro-Wilk normality test: $p=.01283$. C: Residuals for OLS regression on right toothrow length and palate length (seal only). Results of S-W normality test: $p=.0006875$.



S2: Q-Q plots for ANOVAs that are not normally distributed (un-normalized).

Residuals for the ANOVA of mean right tooththrow length between species. Results of Shapiro-Wilk normality test: $p=1.358e-05$. B: Residuals for the ANOVA of left tooththrow length across species. Results of Shapiro-Wilk normality test: $p=3.952e-14$. C: Residuals for the ANOVA of blade length between species. Results of S-W normality test: $9.913e-06$. D: Residuals for the ANOVA of TSA across species. Results of Shapiro-Wilk normality test: $p=0.002008$



S3: Q-Q plots for ANOVAs that are not normally distributed (normalized). A: Residuals for the ANOVA of mean right tooth row length between species. Results of Shapiro-Wilk normality test: $p = 2.385e-06$. B: Residuals for the ANOVA of blade length between species. Results of S-W normality test: $p = 0.005841$. C: Residuals for the ANOVA of TSA across species. Results of Shapiro-Wilk normality test: $p = 3.606e-09$