

UCLA

UCLA Electronic Theses and Dissertations

Title

Morphology and Function of Pinniped Necks: The Long and Short of It

Permalink

<https://escholarship.org/uc/item/0z63g3fn>

Author

Keller, Justin

Publication Date

2019

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

Morphology and Function of Pinniped Necks:

The Long and Short of It

A thesis submitted in partial satisfaction
of the requirements for the degree of Master of Science
in Biology

by

Justin Keller

2019

© Copyright by

Justin Keller

2019

ABSTRACT OF THESIS

Morphology and Function of Pinniped Necks: The Long and Short of It

by

Justin Keller

Master of Science in Biology

University of California, Los Angeles, 2019

Professor Blaire Van Valkenburgh, Chair

Terrestrial vertebrates from at least 30 distinct lineages in both extinct and extant clades, including archosaurs, lepidosaurs, and mammals, have returned to aquatic environments. With these transitions came numerous morphological and physiological adaptations to accommodate life in water. The axial and appendicular skeleton are of particular interest in this transition due to their role in locomotion. Although several studies have focused on the limbs and thoracolumbar spine, less attention has been paid to the cervical region. In fully aquatic cetaceans, the cervical vertebrae are compressed or fused, largely because a loss of neck mobility reduces drag. We ask if this pattern of cervical evolution is present in pinnipeds that have more recently invaded a marine habitat but retain some terrestrial habits. Here, we quantitatively compare neck morphology and function in two groups of pinnipeds with different degrees of aquatic adaptation, the Otariidae and Phocidae, as well as between pinnipeds and their terrestrial

arctoid relatives (ursids and mustelids). Using cranial CT scans of museum specimens, we quantified the occipital surface area for neck muscle attachment and also took linear measurements of the cervical vertebrae to capture vertebral size and shape. Results show that the pinnipeds have a relatively larger occipital surface area than ursids and terrestrial mustelids. This suggests that marine carnivorans have enlarged their neck muscles to assist with stabilizing the head during swimming. Within pinnipeds, there are functional differences in cervical morphology between otariids and phocids that coincide with their degree of aquatic adaptation. Otariids are more specialized for terrestrial locomotion than phocids and have relatively longer cervical vertebrae centra that allow for greater neck flexibility. By contrast, phocids are more specialized for aquatic locomotion and consequently have shorter cervical vertebrae and less flexible necks. Findings also suggest there is a direct relationship between neck flexibility and the habitat complexity of where these animals forage. The quantitative measures used in our analysis are applicable to fossil vertebrate taxa, such as *Enaliarctos* or *Allodesmus*, and enable the tracking of progressive adaptations to life in water during the transition from land to sea.

The thesis of Justin Keller is approved.

Michael Alfaro

David Jacobs

Blaire Van Valkenburgh, Committee Chair

University of California, Los Angeles

2019

Table of Contents

Introduction and Background	1
Materials and Methods	4
Results	6
Discussion	8
Tables	13
Figures	16
References	25

List of Tables

Table 1. List of cranial CT specimens	13
Table 2. List of cervical specimens	14
Table 3. Summary statistics	15

List of Figures

Figure 1. Diagram of occipital surface area measurement.....	16
Figure 2. Diagram of cervical linear measurements.....	17
Figure 3. Diagram of otariid and phocid Transverse process length.....	18
Figure 4. Scatterplot of Occiput SA vs Skull Length.....	19
Figure 5. Scatterplot of Centrum area vs length.....	20
Figure 6. Scatterplot of Neural spine height vs skull length.....	22
Figure 7. Scatterplot of atlas transverse process length vs skull length.....	23
Figure 8. Scatterplot of axis neural spine width vs skull length.....	24

Acknowledgements

First and foremost, I would like to thank my thesis advisor Dr. Blaire Van Valkenburgh. Through our 6-year relationship, she has opened my eyes to the field of functional morphology and has played an instrumental role in shaping my career goals as a scientist. Her empathy, patience and kindness have deeply impacted me, and I will always cherish these years that we were able to work together. Thank you for allowing me to study these amazing marine mammals.

I would also like to thank my committee members, Dr. Mike Alfaro and Dr. David Jacobs, for their insights while developing this project and finalizing this manuscript.

Additionally, I would like to thank the studious undergrads that assisted in data collection for this project. Kimia Noura, Megan Hogfeldt and Ian Platt were a joy to mentor and enriched the quality of my research because of their hard work.

I am grateful for the assistance of the collections managers for allowing me to access their specimens for my research. Kathy Molina at the UCLA Donald R. Dickey Bird and Mammal Collection, James Dines at the Los Angeles Natural History Museum and Dr. Chris Conroy at the Museum of Vertebrate Zoology at Berkeley were all incredibly welcoming.

Additionally, I want to thank Dr. Michael McNitt-Gray for allowing me to use his medical equipment at the UCLA Ronald Reagan Medical Hospital to scan additional skulls.

To Dr. Deborah Bird, thank you for our frequent intellectual discussions on pinniped ecomorphology. You always challenged me as a scientist and my work is better because of it.

Finally, I would like to thank my friends for their support during my graduate journey. Dana Williams, Maddi Cowen, Lauren Smith and Elizabeth Reid-Wainscoat were all there for me during the darkest of times. Their love, encouragement and support kept me going during my formative years as a budding scientist. You are all spectacular individuals and I will cherish our time together always.

Introduction and Background

The vertebrate transition from aquatic to terrestrial habitats required profound anatomical changes to accommodate life on land. Changes to the integument, development of lungs, and modification of the axial and appendicular skeleton were all essential for success in the new, much drier environment that also subjected them to increased gravitational forces. In response, tetrapods developed stronger limbs and larger vertebral centra that bore zygapophyses to aid in support of the spine on land. In addition, tetrapods evolved a specialized first cervical vertebra or atlas, that allowed limited head movements (Liem, 2001). Over time, additional anterior vertebra become modified, creating a neck and allowing more complex head movements. Whereas locomotion in water favors stiff or no necks to minimize drag when swimming, the relative ease of moving through air placed many fewer limitations on neck evolution.

Despite the success of vertebrates on land, numerous groups have returned to the sea over the past 250 million years, including archosaurs, lepidosaurs, and mammals (Kelley & Pyenson 2015). Although the land to sea transition requires fewer modifications than the opposite, it is not without challenges. Typically, it requires reduction in the hindlimbs, modifications of the forelimbs to be more paddle like, and compaction of the neck vertebrae (Fish, 1994). Previous work has been done on limb morphology and swimming mechanics and what role these changes played in the expansion into an aquatic environment (Tarasoff, 1972; Gordon, 1983). The role that the mid-lower spine plays in the pinnipeds (seals, sea lions, walruses) has also been examined (Pierce & Hutchinson, 2011; Jones & Pierce, 2016), but the role played by the neck in this transition in various marine mammal groups is poorly understood. A few studies have used cervical morphology to postulate feeding modes of extinct terrestrial felids (Antón &

Galobart,1999; Antón et al., 2004), but none have looked at the role of the neck during aquatic locomotion.

The spine is an ideal candidate for looking at evidence of locomotor function. It transmits loads from the forelimbs, supports the head and determines regional flexibility in the body via zygapophyseal anatomy and centrum shape. Evidence of the tight relationship between spine anatomy, locomotor ability and ecology have been shown in various terrestrial vertebrates at the large and small scale. Mammals with very different locomotor styles, including bats, primates, colugos and sloths, have been shown to have corresponding lumbar differences (Granatosky et al. 2014). Similarities in lumbar anatomy explain postural and behavioral convergences among primates (Johnson, 1998) and within bovids, increased rigidity in the lumbar region is associated with larger body sizes (Halpert et al., 1987). Gal et al. (1993a,b) found that seal lumbar intervertebral joints are very compliant compared to terrestrial mammals, suggesting this is a response to their aquatic lifestyle. Among delphinids, centrum shape and intervertebral joint shape dictates the degree of mobility in the post-cervical spine (Buchholtz et al.,2004; Long et al., 1997). All of the above supports a strong association between locomotor style and vertebral morphology in both aquatic and terrestrial vertebrates.

Mammals have invaded the marine habitat five times, as cetaceans, sirenians, and within three lineages of Carnivora, Ursidae (polar bear), Mustelidae (otters), and pinnipeds (Otariidae [sea lions and fur seals], Phocidae [seals] and Odobenidae [Walruses]) (Uhen, 2007). The most aquatic of these groups, the cetaceans, show extreme modifications for aquatic life such as complete loss of the hindlimbs, paddle like forelimbs, loss of hair, fusiform body shape, and a completely immobile, compressed, and often fused cervical series. The resultant lack of neck mobility reduces drag while swimming and mimics that of fishes, all of which lack necks.

However, unlike the cetacean condition, pinnipeds have flexible necks, and consequently must actively resist bending in this region to reduce drag. Consequently, we expect that pinnipeds will have increased musculature to support the neck during swimming relative to their terrestrial relatives, such as ursids and mustelids. Moreover, there are significant differences within pinnipeds in the degree of neck flexibility that should be reflected in vertebral form and strength. For example, otariids use an oscillatory motion in their forelimbs to generation propulsion while phocids and odobenids rely on undulation of their hindlimbs (Berta, 2015). The otariid swimming mode is associated with a strong and highly flexible neck, whereas the hindlimb dominated phocid mode is associated with a shorter, stiffer neck (Fish, 2003). Previous work (Pierce, 2011) has shown that vertebral centrum dimensions strongly influence the range of motion at intervertebral joints, suggesting that phocid and otariid cervical centrum shape should differ in predictable ways. Relative to phocid cervicals, otariid cervicals are predicted to be relatively larger with taller neural spines for attachment of comparatively large neck muscles. In addition, centrum shape is likely to differ, with otariids having more elongate centra as opposed to more compact centra in phocids.

Materials and Methods

Occiput Surface Area

Occipital surface area measurements were taken on CT scans of 35 skulls from 27 species of arctoid carnivorans (Table 1) using 3Matic 3D imaging software. Surface area was defined by the nuchal margin of the occiput dorsally and laterally extended to the paraoccipital process (Figure 1) and excluded the occipital condyles. To investigate the effect of ecology, taxa were grouped into one of two categories, aquatic or terrestrial. Taxa were categorized by where they forage; animals that feed in water were defined as aquatic and animals that feed on land were defined as terrestrial. Because of this, species such as the polar bear (*Ursus maritimus*) were defined as terrestrial in this study despite their propensity for swimming.

To examine the effect of body size on occiput surface area, we regressed occiput surface area on condylobasal skull length. Skull length was used as a proxy for body size because specimen specific body mass data are quite difficult to obtain for marine mammals.

Cervical Measurements

The cervical vertebrae of 33 pinniped specimens representing 20 species (8 otariid, 12 phocid) were measured from the collections of the Natural History Museum of Los Angeles County, the Museum of Vertebrate Zoology at the University of California, Berkeley, and the University of California, Los Angeles Donald R. Dickey Bird and Mammal Collection (Table 2). The entire cervical series (C1-C7) was measured as well as condylobasal skull length. Cervical measurements were taken that approximated centrum dimensions and muscle attachment size. The linear measurements include centrum length (CL), height (CH,) width (CW) and neural spine height (CNH) (Figure 2). Centrum plate area was calculated as the product of CH and CW.

Element specific measurements were also taken for the atlas (C1) and axis (C2) because the transverse processes of the atlas and neural spine of the axis are attachment sites for muscles involved in neck rotation and flexion. The element specific measurements were: maximum anteroposterior length of atlas transverse process (AtTP) and axis neural spine anteroposterior length (AxANL). AtTP was measured instead of maximum mediolateral width of the transverse processes because the difference between phocids and otariids in this region is largely a posterior expansion of the process in the latter (Figure 3), and AtTP better captured that variation in shape.

Centrum plate area was compared with centrum length to approximate flexibility of the neck. Previous work on the thoracolumbar region shows that the relationship between centrum area and length impacts the degrees of freedom at each intervertebral joint (Jones et al, 2011). Shorter centra with broader plate areas result in a less flexible neck than longer centra with smaller plate areas. CNH, AtTT, AtTP and AxANL were each regressed against skull length to examine the effect of body size on vertebral dimensions, within groups (e.g. phocids, otariids).

Statistical Analyses

All least squares linear regressions were done using the “lm” function in R. The expected slope value under isometry was two for squared parameters (occiput surface area and centrum plate area) versus skull length and was one for linear measures (CNH, AtTT, AtTP and AxANL) versus skull length. Slope and intercept comparisons between habitat groups and family were done using an ANCOVA in the R package “lsmeans” (Lenth, 2016). Residual values between groups (aquatic vs terrestrial or between families) were compared using a Wilcoxon ranked-sum test.

Results

Occiput Surface Area

Occiput surface area scaled similarly and isometrically with skull length in both aquatic and terrestrial taxa (Figure 3, Table 3), but the y-intercept was significantly larger in aquatic taxa (Table 3), indicating that pinnipeds have relatively larger occiput surface areas across all body sizes than their terrestrial relatives. There were some exceptions to this pattern however. The gray seal (*Halichoerus grypus*), leopard seal (*Hydrurga leptonyx*) and Hawaiian monk seal (*Monachus schauinslandi*) all fell on the terrestrial regression line.

Cervical measurements

Centrum plate area scaled isometrically with centrum length in otariids but was positively allometric in phocids (Figure 4a, Table 3), indicating that phocid centrum plate area is relatively larger for a given centrum length in larger than smaller species. Both the y-intercept and slope of the regression were significantly larger in phocids than otariids (Table 3), indicating that phocid centrum plate area is larger than that of otariids across all centrum lengths. The strong positive allometry in phocid centrum plate area is driven by members of the genus *Mirounga* (elephant seals and the largest members of the family Phocidae); when elephant seals are excluded from the analysis the relationship between centrum plate area and centrum length among phocids is not significantly different from isometry, as in otariids (Figure 4b, Table 3).

Neural spine height (CNH) is positively allometric relative to skull length for both otariids and phocids (Figure 5, Table 3). In both families, large individuals have proportionally longer neural spines compared with smaller individuals. The slope was more positive in otariids than phocids but the difference was only marginally significant ($p = 0.08$). However, the y-

intercept was significantly larger in otariids than phocids (Table 3), indicating that CNH tends to be larger in otariids than phocids across all skull lengths. There are some exceptions to this pattern however. The female stellar sea lion (*Otaria byronia*) as well as the female northern fur seal (*Callorhinus ursinus*) both fell on the phocid regression line.

Atlas transverse process length (AtTP) scaled with positive allometry and similarly in both otariids and phocids (Figure 6, Table 3), indicating that larger individuals have proportionally larger AtTP than smaller taxa in both families. However, AtTP is almost always larger in otariids relative to phocids across all body sizes as shown by a significantly higher y-intercept of the otariid regression line relative to that of phocids (Table 3). Exceptions to this pattern did exist however. Female California sea lions (*Zalophus californianus*), northern fur seals (*Callorhinus ursinus*) and both male and female stellar sea lions (*Otaria byronia*) all fell on the phocid regression line.

Axis anteroposterior neural spine length (AxANL) scaled with positive allometry in otariids and isometrically in phocids (Figure 7, Table 3), indicating that larger otariids tend to have longer neural spines. The slopes of the regressions for both families were marginally significant ($p = 0.08$). The y-intercept was significantly greater in otariids than phocids, reflecting the larger neural spine of the axis in otariids across all body sizes (Figure 7, Table 3).

Sexual Dimorphism

Sexual dimorphism is common among otariids, and also in two genera of phocids, one of which is represented in this study (*Mirounga*). In all cases, males exceed females in size and this was apparent in several of our measurements that reflected muscle size and presumably strength, CNH, AtTP and AxANL. (Figures 5-8).

Discussion

As predicted, the pinnipeds had larger occiputs for their skull length than terrestrial arctoids, including ursids and mustelids. This is consistent with pinnipeds having larger areas of attachment for muscles that control head movement, and is likely a response to increased drag experienced by the animals moving forward in water as opposed to air. Holding the head in line with the body as they move forward allows them to maintain their streamlined shape and minimize drag. Whereas fully aquatic cetaceans have solved this problem through extreme reductions in neck flexibility, pinnipeds retain a supple neck and consequently need greater neck strength to control its movement in a fluid medium.

The association between greater occiput area and aquatic habits is also apparent with the terrestrial arctoids, although to a lesser degree. Sea otters (*Enhydra*) have slightly larger occiput area compared to the other sampled mustelids, suggesting that they have similarly evolved greater musculature for controlling head movements in water. However, our sample size is small and this needs to be confirmed with a larger sample.

Although the two pinniped families were similar in relative occiput area, they differed greatly in aspects of their cervical vertebral morphology that have functional significance. For example, phocids have centra that are short anteroposteriorly and broad mediolaterally and dorsoventrally (large centrum plate surface area), resulting in a relatively disc-like shape (snare drum) as opposed to the more elongate tubular (congo drum) shape of otariid centra. More disc-like centra with large centrum plate areas have fewer degrees of freedom at each vertebral joint (Pierce, 2011) and thus less overall neck flexibility. The reduced centrum area in otariids relative to phocids is likely driven by differences in their locomotor styles. In otariids, propulsion is generated by the forelimbs and the neck acts as a rudder to increase torque during turning (Costa,

2002). Otariids also are more flexible along the thoracolumbar spine to aid in this unique locomotor style (Godfrey 1985) In contrast, phocids generate propulsion from their hindlimbs and maintain a relatively rigid neck during locomotion while using their forelimbs to aid in stability (Fish, 1988). The fact that centrum surface area increased more rapidly with centrum length in phocids than otariids suggests that large bodied phocids, such as *Mirounga*, require more robust necks than smaller phocids. Whereas otariids can use their large forelimb flippers to compensate for unwanted head movements, phocids have relatively small forelimbs. Consequently, as phocids evolve larger size and greater body length, the ability of the hindlimbs to control movements at the front end will decrease, selecting for shorter, stiffer necks. Not surprisingly, the more flexible necked otariids had larger transverse processes and neural spines than the shorter necked phocids. A more flexible neck requires larger muscles for the control of movements while swimming. Specifically, the fact that the transverse processes of the atlas extend more posteriorly in otariids than phocids would not only increase muscle attachment area but increase the resting length of the muscle since the muscle is originating farther from the insertion point on the skull. The aforementioned processes(CNH, AtTP, AxANL) act as attachment sites for a number of muscles. CNH approximates attachment area for the m. multifidus which is involved in neck dorsiflexion. AtTP approximates the attachment of the m. obliquus capitis cranialis on the ventral side and the m. obliquus capitis caudalis on the dorsal side of the process. These muscles are involved in head dorsiflexion and ventroflexion respectively as well as lateral flexion of the head when used bilaterally. AxANL approximates the attachment area of the m. obliquus capitis caudalis (lateral surface) and m. rectus capitis (dorsal border of spine). These muscles are involved in neck rotation and dorsiflexion, respectively. The posterior end of the axis neural spine also acts as an attachment site for the m.

multifidus but AxANL does not capture this. However CNH of the axis approximates this as it does for C3-C7. Therefore, having larger muscle attachment areas would aid in strengthening these motions as well as allow for more control, and consequently, otariids have increased control and stability in this region in every direction (dorsiflexion, ventroflexion, rotation). The large degree of strength and control of the otariid head and neck allows these mammals to locomote in a unique way. Not only would does it allow them to turn faster when needed, but they can also use these muscle groups in concert to maintain a streamlined shape while cruising.

At least two factors likely influence the difference in flexibility within and between families. The first is the habitat complexity of the environments in which they forage, and the second is how they locomote on land. Chasing a prey item in a complex environment, such as a kelp forest or tropical reef, requires agility. Prey items frequently dart sideways to retreat into complex habitat for cover. This is exemplified by all of the otariids in this study, as they forage close to the shore where there is greater habitat complexity (Bowen, 2009). Even within the phocids, the species that have neck flexibility akin to that of similarly sized otariids, such as the harbor seal or monk seal, forage in near shore complex habitats (Bowen, 2009). In less complex environments, like the open ocean, prey items rely on speed instead of agility to avoid capture. Therefore, catching these prey items requires less agility and more speed, favoring a less flexible neck with reduced drag. All members of the genus *Mirounga* forage in the open ocean (Bowen, 2009) and the observed relative inflexibility of their necks makes sense because they forage in an environment with minimal complexity. An association between habitat complexity and neck flexibility is also observed in odontocetes. A majority of the toothed whales forage in the open ocean and have completely immobile necks, which are useful when pursuing prey in a relatively straight line. However, the river dolphin, *Inia geoffrensis*, is an exception among cetaceans.

River dolphins forage in shallow habitats with high complexity, such as flooded forests or rivers, and maintain some flexibility in their neck to aid in catching prey that avoid them with rapid, evasive turns (Fish 2002). The correlation between increased neck flexibility and greater habitat complexity in both pinnipeds and cetaceans suggests strong and similar selection pressure on foraging ability on both groups.

As noted above, the contrast between phocids and otariids in neck morphology might also reflect differences in how they locomote on land. Compared with phocids, otariids are less specialized for aquatic life and employ all four limbs to move on land (sometimes rapidly) while using their necks to hold their heads well above the substrate. Phocids cannot rotate their hindlimbs under their body and instead move by rapid dorsoventral undulations of their whole body, or galumphing, with their head in line with their body and close to the ground. The locomotor differences between phocids and otariids both on land and in water suggest that the neck is playing a very different functional role in each group. The more aquatic phocids have less flexible necks because of their increased reliance on aquatic life relative to pinnipeds. This stark contrast between the two pinniped families suggests that these groups have solved the problem of mitigating drag at the leading edge of the organism in two different ways. Reduced flexibility allows the organism to passively maintain rigidity in a fluid medium as seen in phocids. However, because otariids take advantage of the neck to aid in turning as well as terrestrial locomotion, they maintain rigidity by actively contracting the muscles for neck and head support.

It may be that otariids and phocids have taken alternative evolutionary paths that result in greater ecological separation and reduced competition. Otariids tend to forage nearshore in more structurally complex habitats and so retain a flexible neck. They use their muscular, long

necks to aid in turning while swimming as well as when moving on land. However, the cost of retaining such a large neck might be reductions in maximum speed and greater energetic costs of swimming relative to phocids. Phocids have committed to a more fully aquatic body form and are probably more efficient swimmers. They tend to forage in more open water and thus may feed on different prey than otariids. A number of studies have looked at the relationship between diet and morphology in pinnipeds but due to the large amount of convergence in this group, particularly in phocids, direct ecomorphological inferences are difficult (Kiene, 2018. Adam, 2002). Some pinniped species will alter their feeding behavior depending on the foraging environment (Hocking, 2014), as well as the behavior of the prey (Bowen, 2002). However, there are no data on actual or potential dietary overlap among pinnipeds, so it is not yet possible to assess levels of competition between the two families. To better understand the functional significance of neck morphology in phocids and otariids, we need more data on dietary and foraging differences, as well as quantitative estimates of top speed, agility, and costs of locomotion on land and in water. Once we can tease apart the ecological factors that drive the observed neck flexibility in extant groups, we can then begin to investigate the feeding and locomotor ecology of extinct groups. If robust correlates between ecology and morphology are established, inferences based on specimens that are highly damaged or incomplete, common in the fossil record, can be more readily made. We look forward to revisiting the question of neck variation in pinnipeds in light of these new data.

Tables

Species	Species Code	Family	N	Habitat
<i>Mephitis mephitis</i>	MME	Mustelidae	1(F)	Terrestrial
<i>Mustela frenata</i>	MFR	Mustelidae	2(1F,1M)	Terrestrial
<i>Neovision vison</i>	NVI	Mustelidae	1(U)	Terrestrial
<i>Taxidea taxus</i>	TTA	Mustelidae	2(1F,1M)	Terrestrial
<i>Gulo gulo</i>	GGU	Mustelidae	2(1F1M)	Terrestrial
<i>Enhydra lutris</i>	ELU	Mustelidae	2(1F,1M)	Aquatic
<i>Lontra canadensis</i>	LCA	Mustelidae	2(1F,1M)	Aquatic
<i>Odobenus rosmarus</i>	ORO	Odobenidae	1(U)	Aquatic
<i>Otaria byronia</i>	OBY	Otariidae	1(F)	Aquatic
<i>Arctocephalus pusillus</i>	APU	Otariidae	1(U)	Aquatic
<i>Halichoerus grypus</i>	HGR	Otariidae	1(M)	Aquatic
<i>Zalophus californianus</i>	ZCA	Otariidae	2(1F,1M)	Aquatic
<i>Arctocephalus townsendii</i>	ATO	Otariidae	1(U)	Aquatic
<i>Arctocephalus australis</i>	AAU	Otariidae	1(U)	Aquatic
<i>Phoca vitulina</i>	PVI	Phocidae	1(U)	Aquatic
<i>Hydrurga leptonyx</i>	HLE	Phocidae	1(F)	Aquatic
<i>Mirounga angustirostris</i>	MAN	Phocidae	1(F)	Aquatic
<i>Monachus tropicalis</i>	MTR	Phocidae	1(F)	Aquatic
<i>Erignathus barbatus</i>	EBA	Phocidae	2(1U,1F)	Aquatic
<i>Mirounga leonina</i>	MLE	Phocidae	1(M)	Aquatic
<i>Phoca fasciata</i>	PFA	Phocidae	1(U)	Aquatic
<i>Phoca vitulina</i>	PVI	Phocidae	1(U)	Aquatic
<i>Ailuropoda melanoleuca</i>	AME	Ursidae	1(U)	Terrestrial
<i>Ursus americanus</i>	UAM	Ursidae	1(M)	Terrestrial
<i>Ursus arctos</i>	UAR	Ursidae	1(F)	Terrestrial
<i>Ursus maritimus</i>	UMA	Ursidae	2(2M)	Terrestrial

Table 1

List of species used in Occipital CT scan measurements. Species code, Family sex and Habitat(i.e. terrestrial vs aquatic) is listed for each species. U in the sex column specifies that no sex was listed for the specimen.

Species	Species Code	Family	N
<i>Arctocephalus pusillus</i>	APU	Otariidae	2(1F,1M)
<i>Arctocephalus townsendii</i>	ATO	Otariidae	3(1M,2F)
<i>Callorhinus ursinus</i>	CUR	Otariidae	1(M)
<i>Emetopias jubatus</i>	EJU	Otariidae	3(1M,2F)
<i>Otaria byronia</i>	OBY	Otariidae	2(1F,1M)
<i>Zalophus californianus</i>	ZCA	Otariidae	4(2F, 2M)
<i>Leptonychotes weddelli</i>	LWE	Phocidae	1(F)
<i>Lobodon carcinophaga</i>	LCA	Phocidae	2(F)
<i>Mirounga leonina</i>	MLE	Phocidae	2(1F,1M)
<i>Monachus schauinslandi</i>	MSC	Phocidae	1(F)
<i>Phoca vitulina</i>	PVI	Phocidae	3(M)
<i>Pusa hispida</i>	PHI	Phocidae	1(U)
<i>Pusa sibirica</i>	PSI	Phocidae	1(F)
<i>Erignathus barbatus</i>	EBA	Phocidae	1(M)
<i>Halichoerus grypus</i>	HGR	Phocidae	2(1F,1M)
<i>Mirounga angustirostris</i>	MAN	Phocidae	4(2F,2M)

Table 2

List of species used for cervical measurements. Species code, Family and sex is listed for each species. U in the sex column specifies that no sex was listed for the specimen.

Regression	n	Group	Slope(b)	y-intercept	R ²	CI of Slope
<i>Occiput SA vs Skull Length</i> ⁺	26	Aquatic	2.03	-1.91	0.89	1.87-2.48
	14	Terrestrial	2.13	-2.84	0.97	1.94-2.42
Centrum Area vs Length ⁺ ◆	14	Otariidae	1.70	0.17	0.88	1.46-2.26
	18	Phocidae	2.5*	0.86	0.92	2.23-3.06
Centrum Area vs Length(w/o <i>Mirounga</i>) ⁺	13	Phocidae	2.09	-0.29	0.88	1.75-2.80
NS Height vs Skull Length ⁺	14	Otariidae	1.43*	-1.63	0.87	1.22-1.92
	18	Phocidae	1.14*	-1.11	0.96	1.04-1.31
Atlas TP Length vs Skull Length ⁺	14	Otariidae	1.30*	-1.24	0.78	1.10-1.98
	18	Phocidae	1.35*	-1.46	0.98	1.25-1.49
Axis NS Length vs Skull Length ⁺	14	Otariidae	1.47*	-1.80	0.78	1.25-2.25
	18	Phocidae	1.05	-0.89	0.78	0.93-1.54

Table 3

Summary statistics from regressions used in this study. * indicates a significant difference ($p < 0.05$) in slope from expected values of 2 for Occiput SA and centrum area and 1 for remaining regressions. ◆ indicates a significant difference ($p < 0.05$) in slope between groups (habitat or family). + indicates a significant difference ($p < 0.05$) in intercept between groups.

Figures

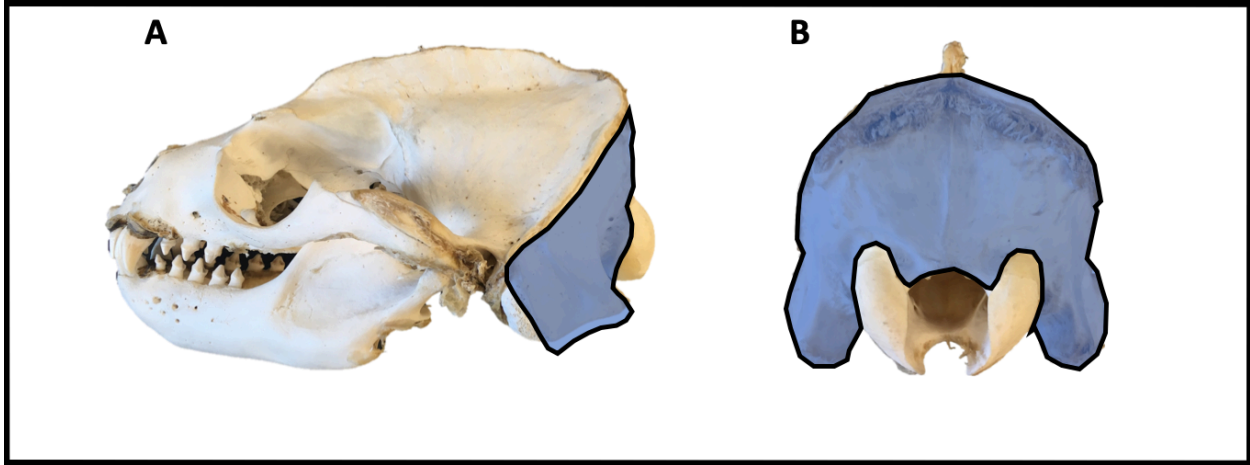


Figure 1
Visual representation of the surface area measurement for this study. [A] lateral and [B] posterior view of a *Zalophus* skull with occiput surface area represented in blue.

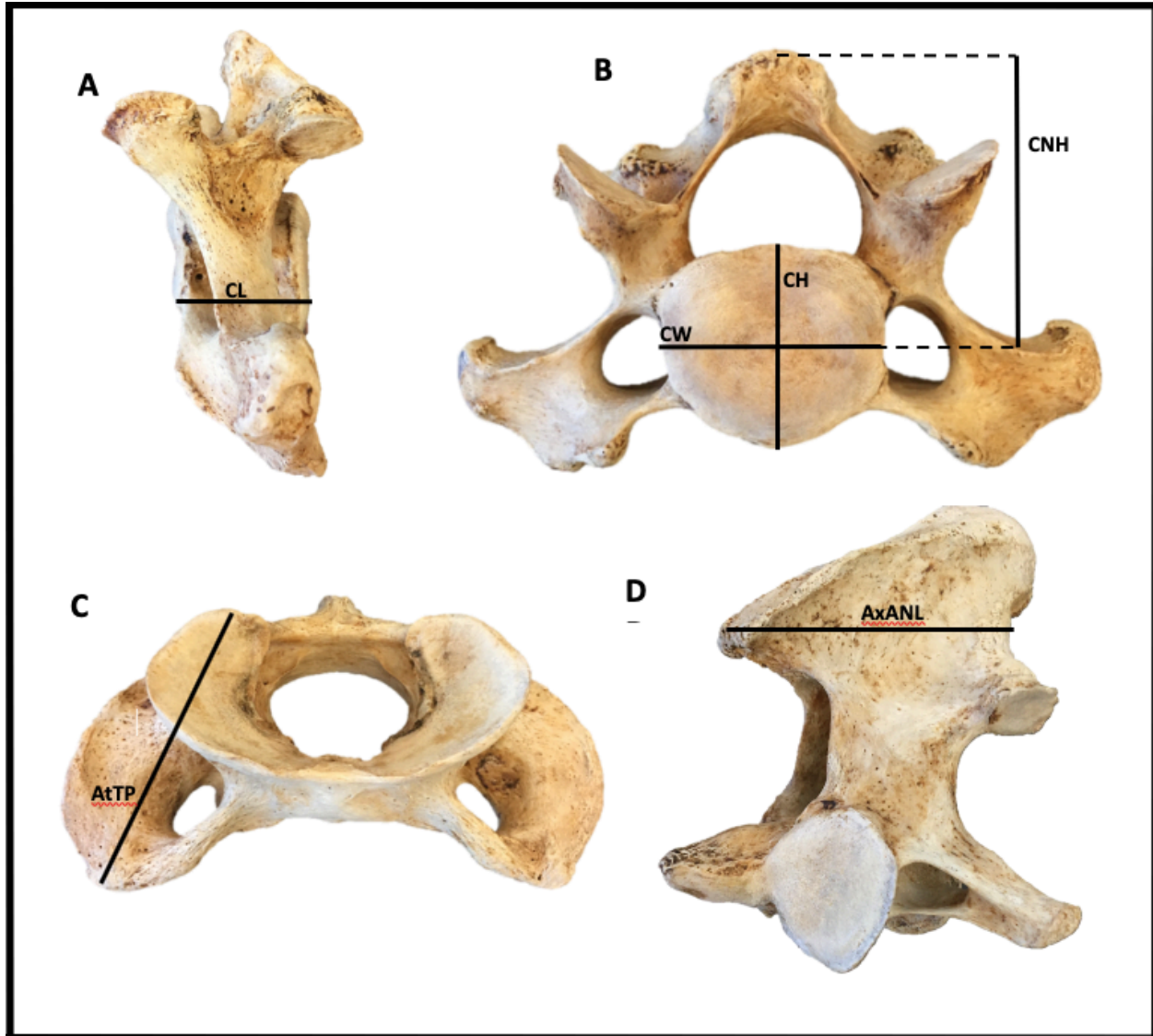


Figure 2

Visual representation of the linear measurements for this study. Cervical vertebrae of *Odobenus*: [A] Lateral view of C3 with centrum length (CL); [B] Anterior view of C3 with centrum width (CW), centrum height (CH) and centrum base to neural spine length (CNL); [C] anterior view of atlas with maximum lateral transverse process width (AtTP); [D] Axis neural spine width (anteroposterior).

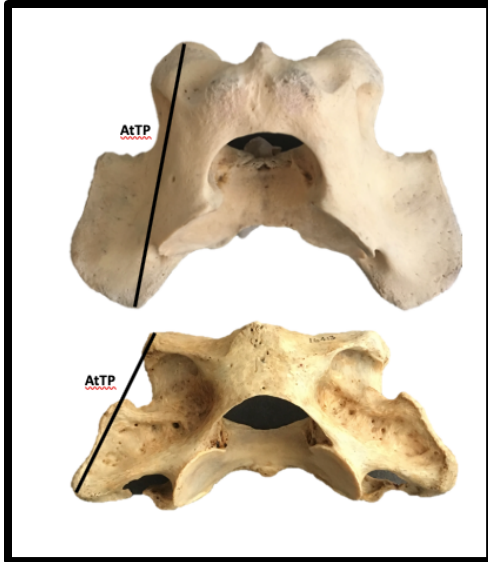


Figure 3

Dorsal view of two atlas vertebrae for an otariid (*E. jubatus*) (**top**) and phocid (*E. barbatus*) (**bottom**) showing the AtTP measurement used in this study. Note the expansion of the transverse process in the posterior direction in the otariid compared to the phocid.

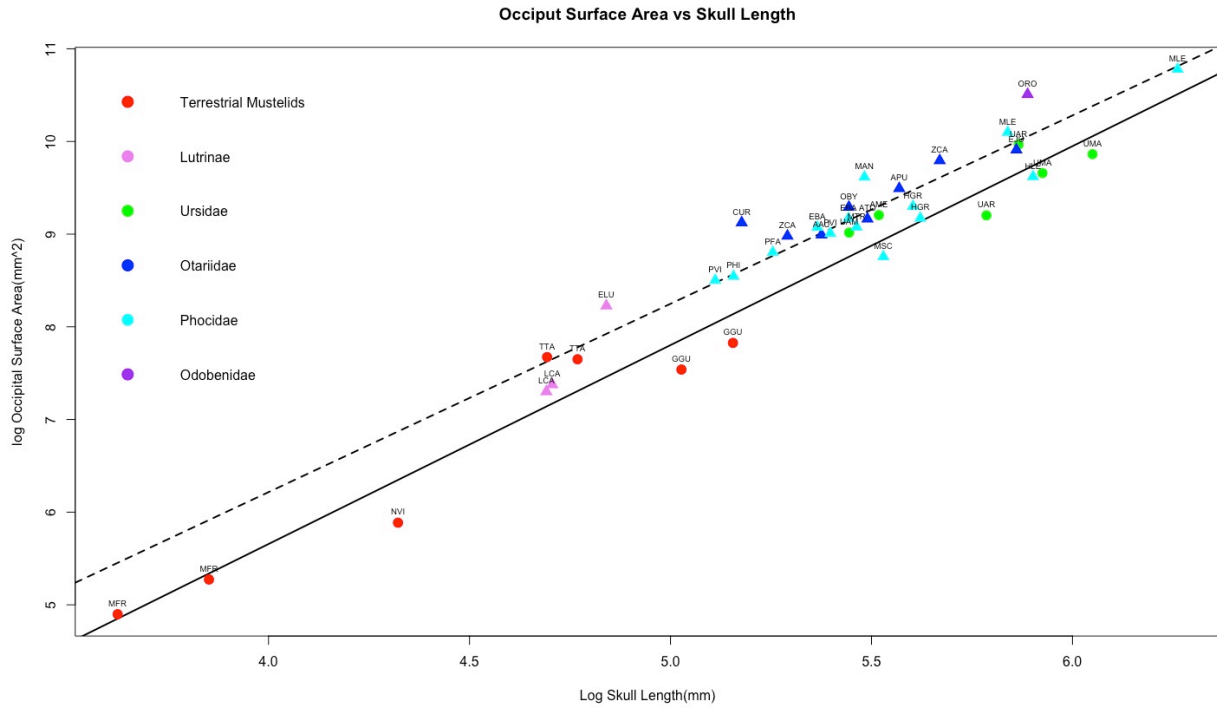


Figure 4
 Scatterplot of occipital surface area vs skull length. Aquatic taxa(triangles) and corresponding regression(dotted), terrestrial taxa(circles) and corresponding regression(solid). Families are differentiated by color (see legend). See table 4 for line equations and regression statistics.

Centrum Area vs Length

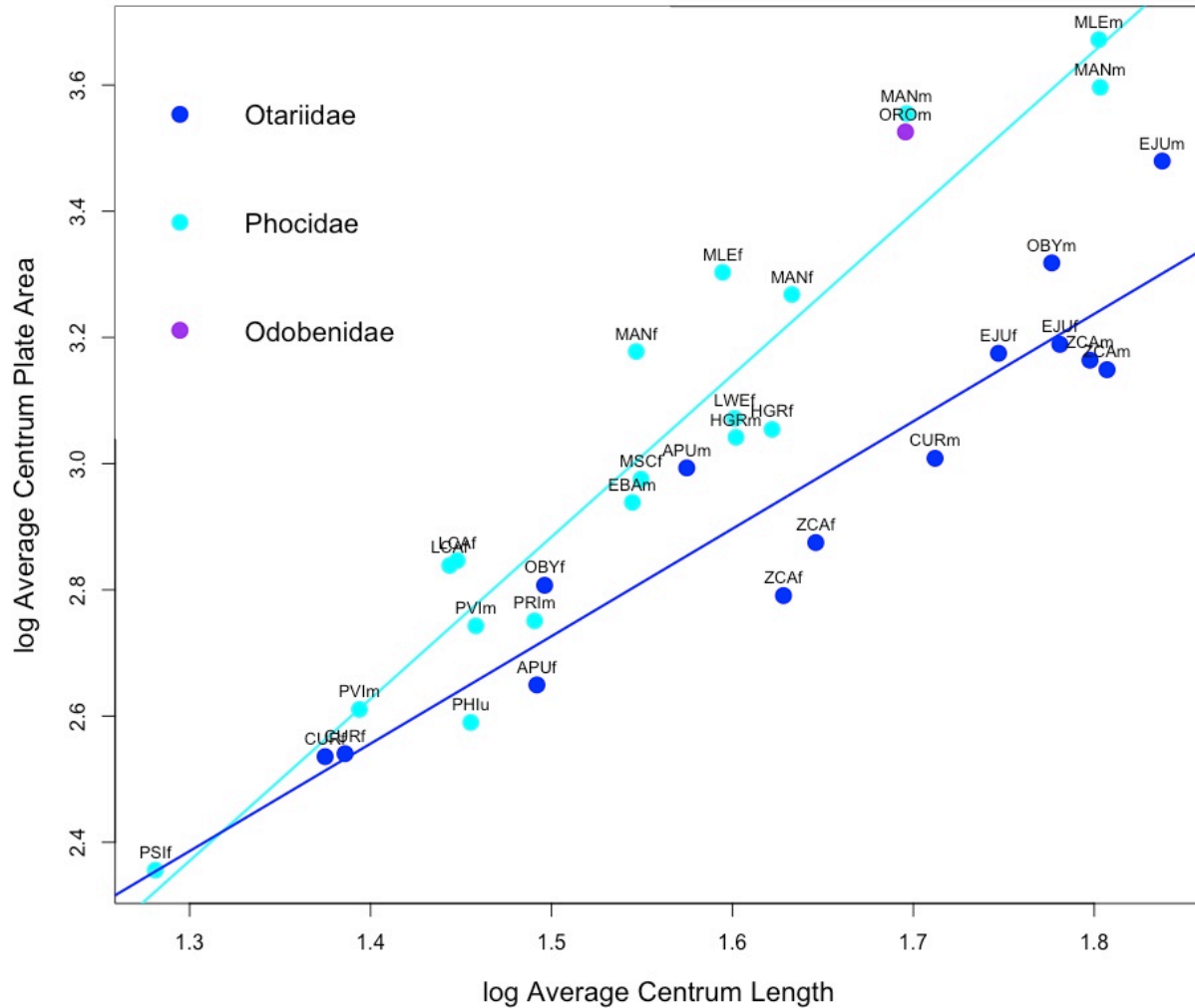


Figure 5a
 Scatterplot of centrum area vs length within Pinnipedia. Values were averaged across C2-C7 and log corrected to fit a linear model (black line). Species labels from Table 1. Regression lines: total (black), Otariidae (dark blue) and Phocidae (light blue). Families are denoted by dark blue (Otariidae), light blue (Phocidae) and purple (Odobenidae). The lower case letters after the species code denote sex (m: Male, f: Female, u: Undefined). See table 4 for line equations and regression statistics.

Centrum Area vs Length(Excluding Mirounga)

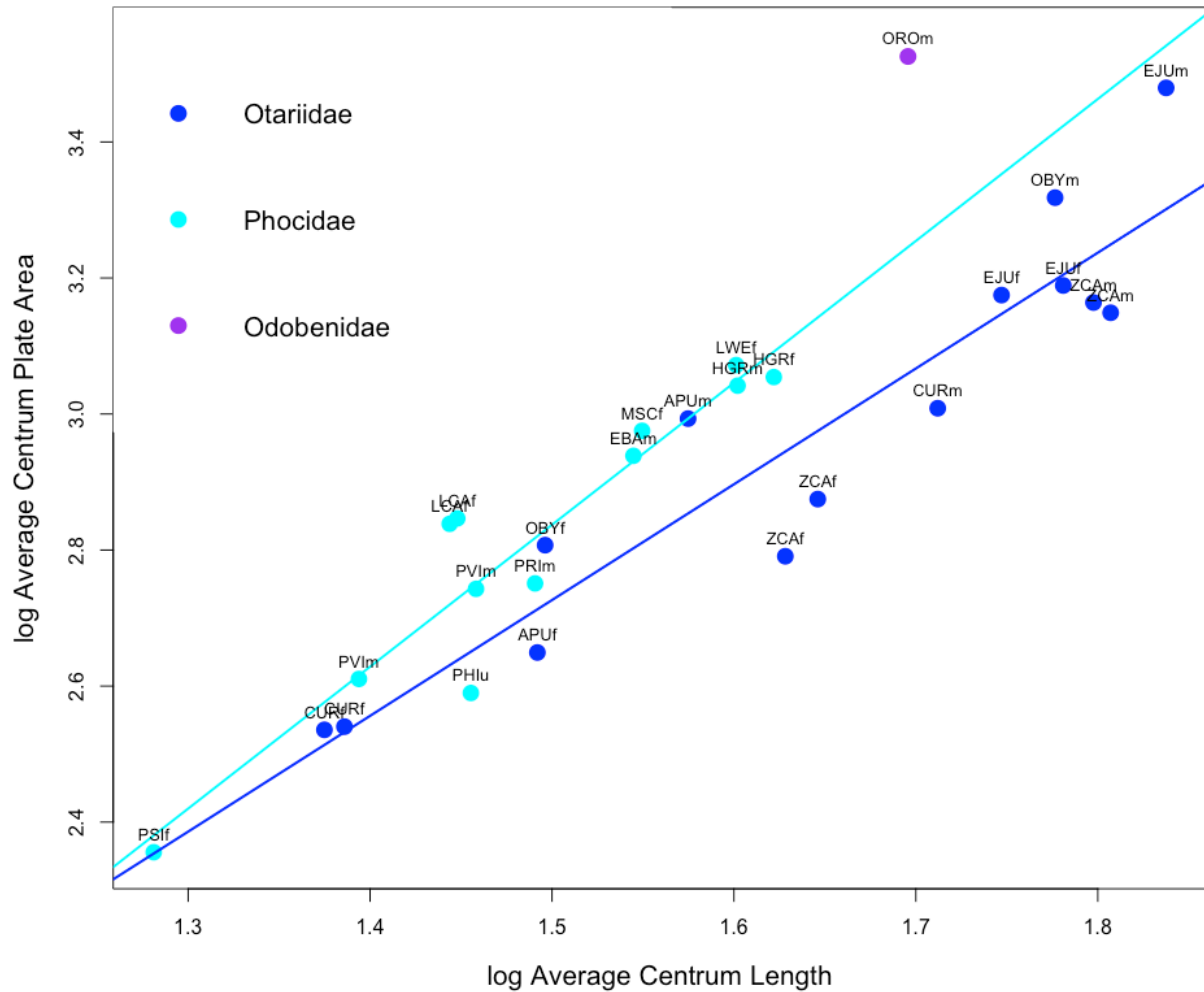


Figure 5b

Scatterplot of centrum area vs length within Pinnipedia excluding members of the genus *Mirounga*. Values were averaged across C2-C7 and log corrected to fit a linear model (black line). Regression lines: total (black), Otariidae (dark blue) and Phocidae (light blue). Families are denoted by dark blue (Otariidae), light blue (Phocidae) and purple (Odobenidae). The lower case letters after the species code denote sex (m: Male, f: Female, u: Undefined). See table 4 for line equations and regression statistics.

Neural Spine Height vs Body Size

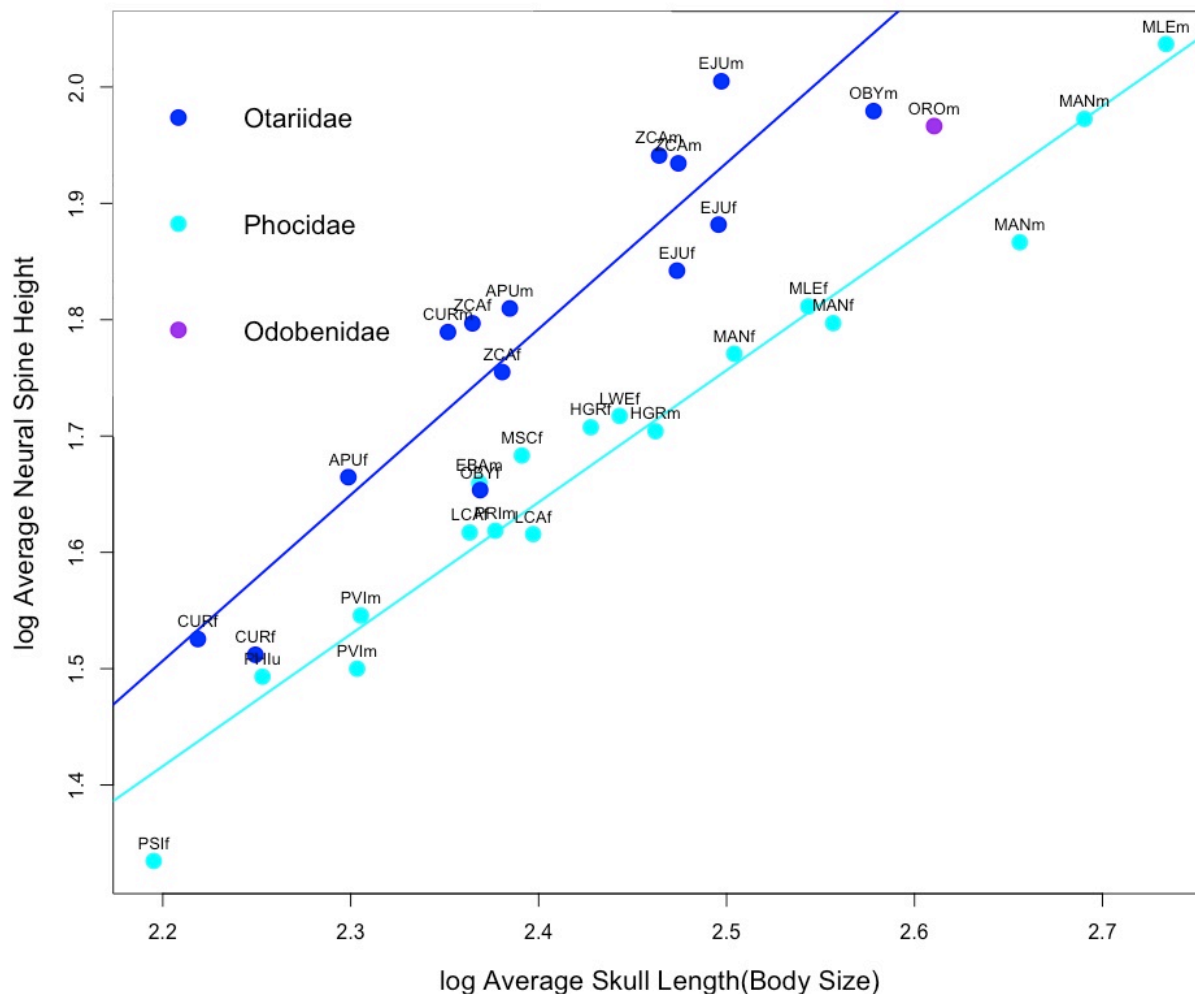


Figure 6

Scatterplot of neural spine height vs skull length within Pinnipedia. Values were averaged across C2-C7 and log corrected to fit a linear model (black line). Species labels from Table 1. Regression lines: total (black), Otariidae (dark blue) and phocidae (light blue). Families are denoted by dark blue (Otariidae), light blue (Phocidae) and purple (Odobenidae). The lower case letters after the species code denote sex (m: Male, f: Female, u: Undefined). See table 4 for line equations and regression statistics.

Atlas Transverse process Length vs Skull Length

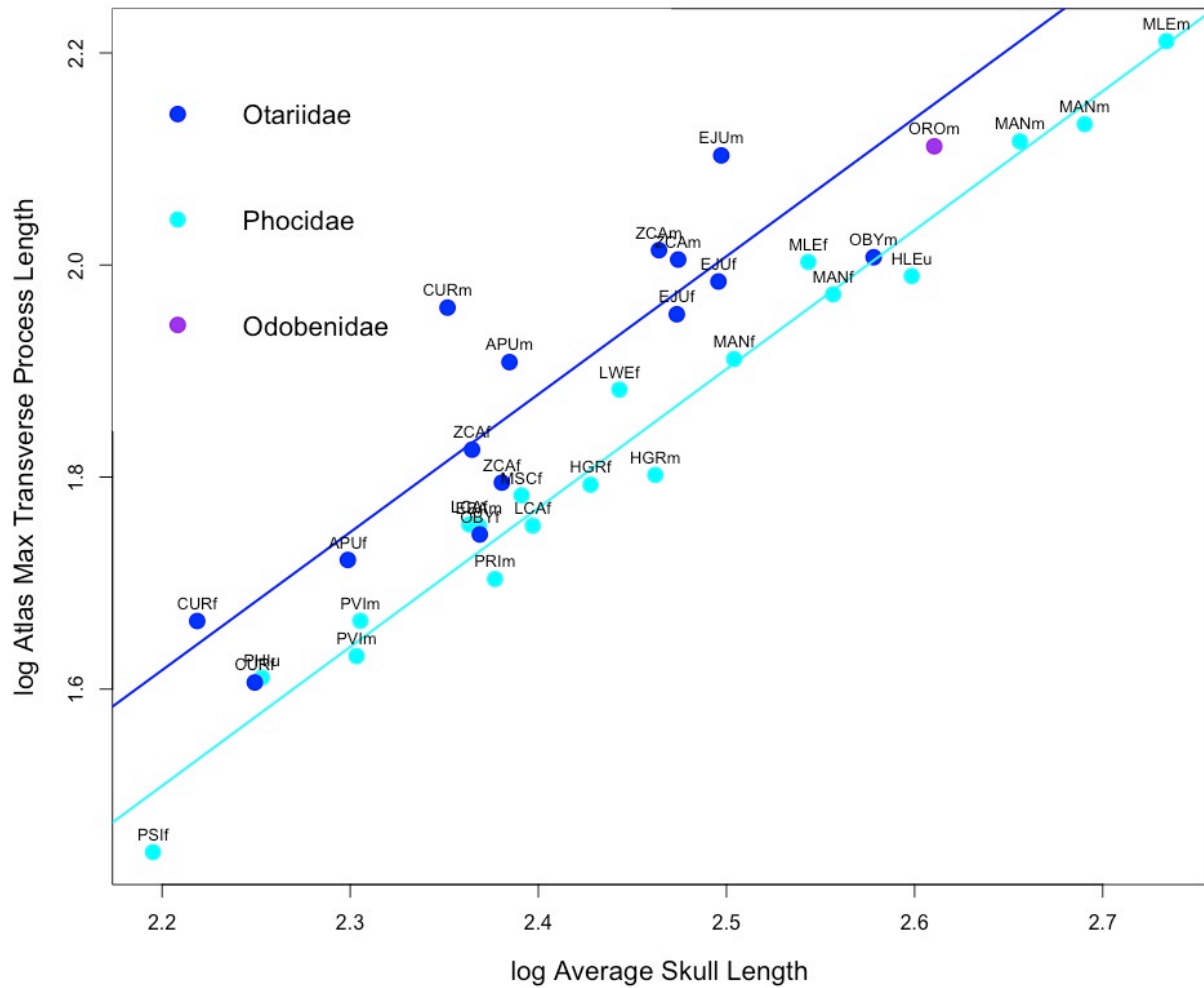


Figure 7

Scatterplot of atlas transverse process length vs skull length within Pinnipedia. Values log corrected to fit a linear model(black). Species labels from Table 1. Regression lines: total(Black), Otariidae(dark blue) Phocidae(light blue) . Families are denoted by dark blue(Otariidae), light blue(Phocidae) and purple(Odobenidae). The lower case letters after the species code denote sex(m:Male, f:Female, u:Undefined). See table 4 for line equations and regression statistics.

Axis Neural Spine Length vs Skull Length

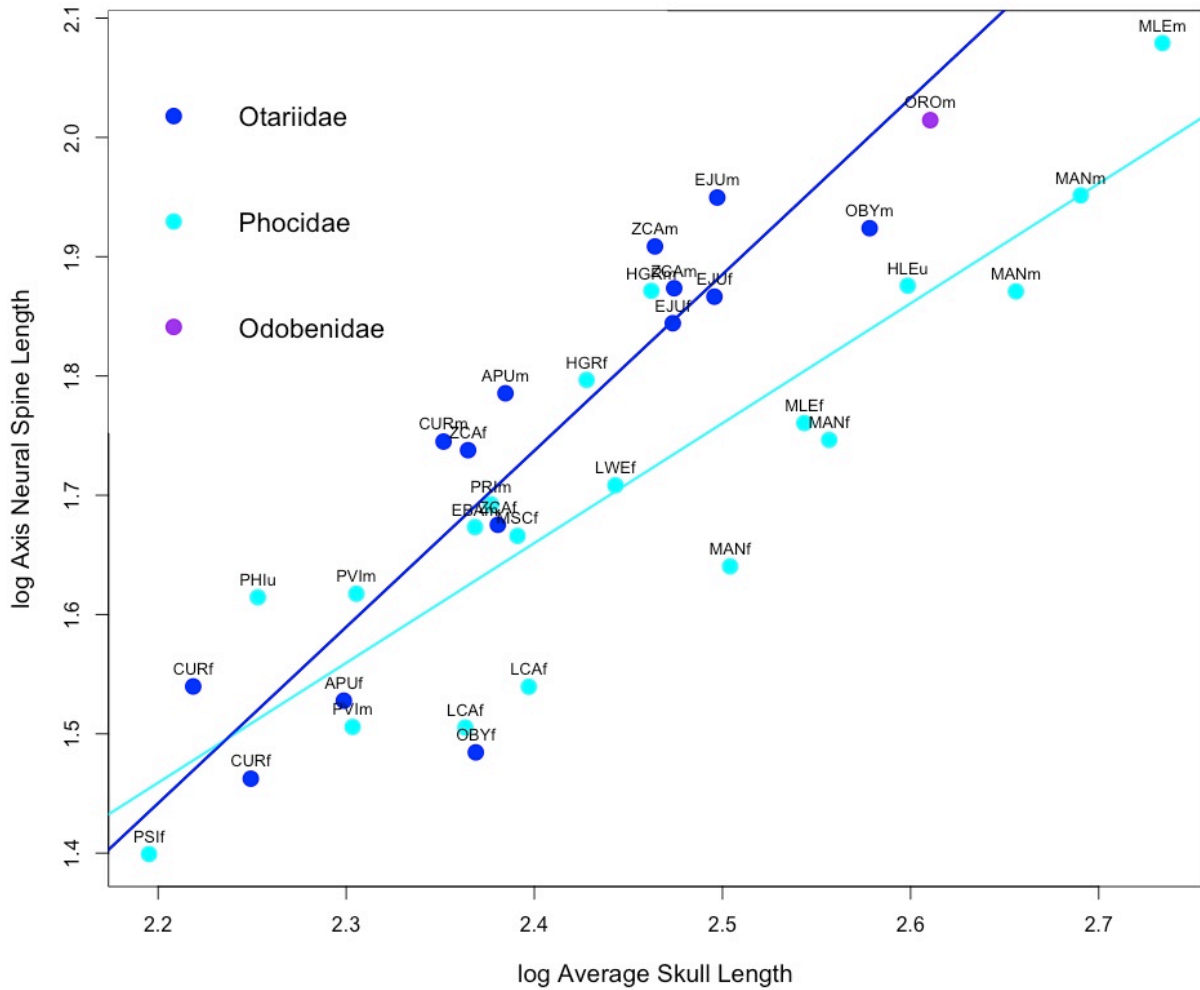


Figure 8

Scatterplot of axis neural spine length vs skull length within Pinnipedia. Values log corrected to fit a linear model(black). Species labels from Table 1. Regression lines: Total(Black), Otariidae(dark blue) and Phocidae(light blue). Families are denoted by dark blue(Otariidae), light blue(Phocidae) and purple(Odobenidae). The lower case letters after the species code denote sex(m:Male, f:Female, u:Undefined). See table 4 for line equations and regression statistics.

References

- Adam, P. J. & Berta, A. (2002). Evolution of prey capture strategies and diet in the Pinnipediomorpha (Mammalia, Carnivora). *Oryctos*, **4**, 83-107.
- Antón, M., & Galobart, À. (1999). Neck function and predatory behavior in the scimitar toothed cat *Homotherium latidens* (Owen). *Journal of Vertebrate Paleontology*, **19(4)**, 771-784.
- Antón, M., Salesa, M. J., Pastor, J. F., Sanchez, I. M., Fraile, S., & Morales, J. (2004). Implications of the mastoid anatomy of larger extant felids for the evolution and predatory behaviour of sabretoothed cats (Mammalia, Carnivora, Felidae). *Zoological Journal of the Linnean Society*, **140(2)**, 207-221.
- Berta, A., Sumich, J. L., Kovacs, K. M. (2015). *Marine Mammals(Third Edition)*, Academic press.
- Bowen, W. D., Beck, C. A., Austin, D. A. (2009). *Encyclopedia of Marine Mammals(Second Edition)*, Academic press.
- Bowen, W.D., Tully, D., Boness, D. J., Bulheier, B. M., and Marshall, G. J. (2002). Prey dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.*, **244**, 235-245
- Buchholtz, E. A., & Schur, S. A. (2004). Vertebral osteology in Delphinidae (Cetacea). *Zoological Journal of the Linnean Society*, **140(3)**, 383-401.
- Fish, F. E. (1994). Influence of hydrodynamic-design and propulsive mode on mammalian swimming energetics. *Australian Journal of Zoology*, **42(1)**, 79-101.
- Fish, F. E. (2002). Balancing requirements for stability and maneuverability in cetaceans. *Integ. Comp. Biol.* **42**, 85-93.
- Fish, F. E., Hurley, J., Costa, D. P., Chester, W., & Marine, M. L. (2003). Maneuverability by the sea lion *Zalophus californianus* : turning performance of an unstable body design, (2002), 667–674. <https://doi.org/10.1242/jeb.00144>
- Gal, J.M. (1993a). Mammalian spinal biomechanics. I. Static and dynamic mechanical properties of intact intervertebral joints. *J. Exp. Biol.* **174**, 247-280.
- Gal, J.M. (1993). Mammalian spinal biomechanics. II Intervertebral lesion experiments and mechanisms of bending resistance . *J. Exp. Biol.* **174**, 281-297.
- Gordon, K. R. (1983). Mechanics of the limbs of the walrus (*Odobenus rosmarus*) and the California sea lion (*Zalophus californianus*). *Journal of Morphology*, **175(1)**, 73-90.

- Granatosky, M. C., Miller, C. E., Boyer, D. M., & Schmitt, D. (2014). Lumbar vertebral morphology of flying, gliding, and suspensory mammals: Implications for the locomotor behavior of the subfossil lemurs *Palaeopropithecus* and *Babakotia*. *Journal of human evolution*, **75**, 40-52.
- Halpert, A. P., Jenkins, F. A., & Franks, H. (1987). Structure and scaling of the lumbar vertebrae in African bovids (Mammalia: Artiodactyla). *Journal of Zoology*, **211**(2), 239-258.
- Hocking, D. P., M. Salverson, E. M. Fitzgerald, and A. R. Evans. (2014). Australian fur seals (*Arctocephalus pusillus doriferus*) use raptorial biting and suction feeding when targeting prey in different foraging scenarios. *PLoS ONE*, **9**, e112521.
- Johnson, S. E., & Shapiro, L. J. (1998). Positional behavior and vertebral morphology in atelines and cebines. *American journal of physical anthropology*, **105**(3), 333-354.
- Jones, K. E., & Pierce, S. E. (2016). Axial allometry in a neutrally buoyant environment: effects of the terrestrial-aquatic transition on vertebral scaling. *Journal of evolutionary biology*, **29**, 594-601.
- Kelley, N. P., & Pyenson, N. D. (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science*, **348**(6232).
<https://doi.org/10.1126/science.aaa3716>
- Kienle, S. S., Hermann-Sorensen, H., Costa, D. P., Reichmuth, C., Mehta, R. S. (2018). Comparative feeding strategies and kinematics in phocid seals: suction without specialized skull morphology. *Journal of Experimental Biology*. **221**, jeb-179424
- Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *J. Stat. Softw.* **69**, 1-33.
- Liem, K.F, W.E. Bemis, W.F. Walker, Jr., and L. Grande. (2001). *Functional Anatomy of the Vertebrates: An Evolutionary Perspective (3rd Edition)*. Cengage Learning.
- Long, J. H., Pabst, D. A., Shepherd, W. R., & Mclellan, W. A. (1997). Locomotor design of dolphin vertebral columns: bending mechanics and morphology of *Delphinus delphis*. *Journal of Experimental Biology*, **200**(1), 65-81.
- Pierce, S. E., Clack, J. A., & Hutchinson, J. R. (2011). Comparative axial morphology in pinnipeds and its correlation with aquatic locomotory behaviour. *Journal of anatomy*, **219**(4), 502-514.
- Tarasoff, F. J. (1972). Comparative aspects of the hind limbs of the river otter, sea otter and seals. *Functional anatomy of marine mammals*, **1**, 333-359.
- Uhen, M. D. (2007). Evolution of marine mammals: back to the sea after 300 million years. *The anatomical record*, **290**(6), 514-522.