

INFERRING SWIMMING MODE FROM SKELETAL PROPORTIONS IN FOSSIL PINNIPEDIMORPHS

Introduction

Since the first vertebrates invaded the terrestrial realm around 350 million years ago (Clack 2002a, 2002b; Long and Gordon 2004), several subsequent groups of tetrapods have become readapted for an aquatic lifestyle (Mazin and de Buffrénil 2001). Among mammals, the spectrum of secondarily aquatic forms ranges from fully aquatic cetaceans and sirenians to semiaquatic taxa that spend much of their time on land but forage in the water (Gingerich 2003). One of the most speciose groups of secondarily aquatic mammals today, composed of about 36 extant species, is the Pinnipedia (Berta and Adam 2001; Berta et al. 2006). Pinnipeds are highly derived, mostly aquatic mammals within the Order Carnivora and are divided into three modern families: Odobenidae (walruses), Otariidae (sea lions and fur seals), and Phocidae (true or earless seals) (Berta et al. 2006). Based on morphological and paleontological evidence, pinnipeds were traditionally thought to have a diphyletic origin (McLaren 1960; Tedford 1976). This view maintained that the odobenids and otariids were derived from ursid (bears) ancestry and that phocids had a separate origin from somewhere within the mustelid (weasels, otters, etc.) lineage. Wyss (1987) reassessed the morphological evidence and suggested a common origin for all pinnipeds. A number of morphological (Wyss 1988; Berta et al. 1989; Wyss 1989; Wyss and Flynn 1993; Berta and Wyss 1994) and molecular studies (Sarich 1969; Árnason and Widegren 1986; Vrana et al. 1994; Árnason et al. 1995; Lento et al. 1995; Flynn and Nedbal 1998; Davis et al. 2004; Árnason et al. 2006) have since given strong support for pinniped monophyly, but the arctoid group from which pinnipeds arose has not yet been agreed upon, with studies suggesting ursid (Wyss and Flynn 1993; Berta and Wyss 1994; Vrana et al. 1994; Lento et al. 1995), mustelid (Árnason and Widegren 1986; Flynn and Nedbal 1998), or general arctoid ancestry (Davis et al. 2004; Árnason et al. 2006).

One way in which the pinniped groups significantly differ from each other is how they swim. Otariids swim using a form of locomotion called pectoral oscillation, in which the highly modified fore-flippers are the sole source of thrust while the hind limbs and axial skeleton play no apparent role (English 1976; Feldkamp 1987a, 1987b). Conversely, phocids and odobenids swim using primarily pelvic oscillation, in which the cranial end of the body is held rigid while the hind limbs perform a side-to-side “sculling” motion to generate forward thrust (Tarasoff et al. 1972; Gordon 1981). Both modes of swimming are highly derived and require very specialized morphologies in order to perform them (Fish 1996; Berta and Adam 2001). During the evolutionary transition from land to sea in pinnipeds, taxa intermediate between the fully terrestrial ancestors and the mostly aquatic descendants would have lacked some of these skeletal adaptations and would have swum in a manner different from modern forms. Since locomotion is central to an animal’s ability to forage, evade predators, disperse, and migrate (Fish 1992), understanding how these highly derived modes of locomotion evolved from less efficient modes can inform us about the ecologies and lifestyles of intermediate species and help us understand how the land-to-sea transition progressed.

Models have been proposed to explain how highly derived modes of swimming could have evolved through semiaquatic taxa performing a series of increasingly efficient swimming styles (Fish 1996, 2000, 2001), but these studies have been based primarily on studies of swimming in living aquatic and semiaquatic mammals. Few studies have assessed the evolution of swimming mode in secondarily aquatic taxa using fossil evidence. Berta and Adam (2001) used the morphologies of extant pinnipeds to interpret the locomotor capabilities of extinct forms and placed these swimming styles onto a phylogeny to assess how forelimb- and hind limb-dominated swimming evolved within pinnipeds. Their results suggested: (1) that forelimb-

dominated swimming was ancestral for the group, (2) that hind limb-dominated swimming arose once at the base of the Phocomorpha (the sister group to the Otariidae), and (3) that there was one reversal back to forelimb swimming in the Dusignathinae (Figure 1). However, the interpretations of locomotor mode in some of the fossil taxa in this study (mainly *Enaliarctos* and the Desmatophocidae) are not as straightforward as these authors presented them to be, and their potential locomotor capabilities could stand to be reassessed.

The most primitive known group of pinnipedimorphs is the Enaliarctinae (Barnes 1989, 1990; Berta 1991; Barnes 1992). *Enaliarctos mealsi*, from the late Oligocene of California, is known on the basis of a virtually complete skeleton (Figure 2A-B), and when it was initially described, it was thought to swim using a combination of fore flippers, hind flippers, and undulation of the axial skeleton to generate thrust (Berta et al. 1989; Berta and Ray 1990). However, Berta and Adam (2001) asserted that *Enaliarctos* “seems slightly more specialized for forelimb swimming” (p. 256) and coded this species as being a forelimb-dominated swimmer in their locomotor analysis. To further support this notion, they argued that since this fossil taxon is bracketed by two groups that use forelimb propulsion (the Ursidae and Otariidae) it is most parsimonious to interpret *Enaliarctos* as a forelimb swimmer rather than a hind limb swimmer. This interpretation has persisted in additional sources (e.g. Berta et al. 2006) but has yet to be quantitatively tested.

Likewise, there has been disagreement as to how the desmatophocid *Allodesmus kernensis* swam (Figure 2C). This species is a member of the Desmatophocidae, a group which was once considered to be a subfamily of Otariidae (Mitchell 1966; Barnes 1972; Mitchell 1975; Barnes 1989) but is now thought to be the sister group of the Phocidae (Berta 1994; Berta and Wyss 1994; Deméré and Berta 2002). The initial descriptions of *Allodesmus* postulated it used

solely its forelimbs in aquatic locomotion, much as modern otariids do (Mitchell 1966; Barnes 1972). However, Giffin (1992) demonstrated that the anatomy of the neural canal in this species suggests that its torso, fore-, and hind limbs all possessed significant innervation. This morphology was found to be most similar to odobenids, and Giffin called into question the previous interpretations of forelimb-dominated swimming. Berta and Adam (2001) noted that *Allodesmus* has features indicative of both forelimb and hind limb swimming, but they coded it as being a hind limb swimmer in their locomotor analysis, an interpretation that has persisted in recent references (e.g. Berta et al. 2006).

For at least these two species, there is some question as to whether they swam using primarily forelimb- or hind limb-dominated locomotion, and given their phylogenetic positions in relation to other pinnipedimorph taxa, understanding the evolution of locomotion within the entire group is contingent on having accurate inferences about their swimming mode. Given their relatively complete skeletons, locomotor interpretations for *Enaliarctos* and *Allodesmus* can be tested by including them in a principal components analysis (PCA) on skeletal proportions in extant semiaquatic mammals like that performed by Gingerich (2003). This method has been used to interpret locomotor mode in fossil whales (Gingerich 2003), desmostylians (Gingerich 2005), and pantolestids (Rose and von Koenigswald 2005), and by finding which modern mammals *Enaliarctos* and *Allodesmus* are most similar to in overall skeletal proportions, we will be able to make well-informed inferences about their swimming modes. These results can then be looked at in a phylogenetic context, as was done by Berta and Adam (2001), in order to assess how locomotor evolution occurred in pinnipeds.

Methods

Of the fourteen skeletal measurements included in the PCA performed by Gingerich (2003), thirteen of the measurements for *Enaliarctos* were obtained from Berta and Ray (1990) (Table 1). The missing measurement, the length of pedal phalanx III-2, was estimated by scaling it down from the length of metatarsal III in the same proportion as pedal phalanx II-2 is scaled down in length from metatarsal II. A PCA was carried out on 14 skeletal measurements for 61 extant semiaquatic taxa following the methods described in Gingerich (2003). These 61 taxa included the 50 specimens used by Gingerich (2003), as well as 11 additional pinnipeds and lutrine mustelids to increase the representation of these diverse groups in the data set (Table 1). Eigenvector coefficients for each of most informative principal component axes were multiplied by the normalized, natural log-transformed measurements and summed across all 14 measurements to generate scores for each species for each principal component. *Enaliarctos* was not included in the PCA itself, but was added as a supplemental taxon, following the treatment of fossil taxa in previous analyses (Gingerich 2003, 2005; Rose and von Koenigswald 2005), and was plotted in the same space as the modern taxa using the eigenvector coefficients generated by the PCA to calculate its PC scores. For *Allodesmus*, no pedal phalanges are known, so an additional PCA was carried out using only 12 of the 14 measurements. Measurements for the thorax, lumbus, humerus, radius, femur, and tibia of *Allodesmus* were obtained from tables in Mitchell (1966), while the remaining measurements were estimated from photographic plates therein (Table 1). Like *Enaliarctos*, *Allodesmus* was not included in the PCA itself, but its PC scores were calculated using the eigenvector coefficients resulting from the analysis. The locomotor modes inferred for these two taxa based on the PCAs were then placed onto a phylogeny of pinnipeds to assess when different swimming styles appeared within the history of

the group, thus giving us an overall picture of how this important behavior may have been evolving during this land-to-sea transition.

Results

The first PCA performed in this study included 14 skeletal measurements for 61 extant semiaquatic mammals. The eigenvalues and eigenvector coefficients (loadings) for each principal component are listed in Table 2, with the eigenvector coefficients also being shown graphically in Figures 3-4. The variation in this data set was reduced to three informative axes. PC-I accounted for 93.1% of the total variance in measurements, and all of the eigenvector coefficients are positive and of a similar magnitude. This is very similar to Gingerich's (2003) results, and this axis can best be understood as representing overall size, with smaller individuals possessing more negative PC-I scores and larger individuals possessing more positive PC-I scores. PC-II accounted for 4.2% of the total variance, and the eigenvector coefficients indicate that the strongest contrast on PC-II is between individuals with long manual and pedal phalanges and individuals with a long femur and ilium, just as in Gingerich's (2003) analysis. This axis can thus be interpreted as separating more terrestrial species on the positive end of the axis from more aquatic species on the negative end. PC-III accounted for 0.8% of the total variance, and the eigenvector coefficients indicate that the strongest contrast is between taxa with a long lumbus, a long third metatarsal, and long pedal phalanges and taxa with a long third metacarpal and long manual phalanges. Again, this follows Gingerich's (2003) results, so PC-III can be interpreted as separating hind limb-dominated swimmers with more negative PC-III scores from forelimb-dominated swimmers with more positive PC-III scores. PC scores for each taxon for the first three principal components are listed in Table 4 and shown graphically in Figures 3-4. When the PC scores for *Enaliarctos* are plotted in the same space as the modern taxa, it plots

right with other pinnipeds on the size axis and appears to be less aquatic than the majority of the modern otariids and phocids but more aquatic than *Odobenus* on the terrestrial/aquatic axis. On the locomotion axis, *Enaliarctos* actually plots within the space occupied by the Phocidae, suggesting that *Enaliarctos* was primarily a hind limb-dominated swimmer and calling into question the recent interpretations that this species swam primarily using its forelimbs to generate propulsion.

The second PCA included only 12 skeletal measurements for the 61 extant semiaquatic mammals. The eigenvalues and eigenvector coefficients (loadings) for each principal component are listed in Table 3, with the eigenvector coefficients also being shown graphically in Figures 5-6. The variation in the data was again reduced to three informative axes. PC-I accounted for 93.8% of the total variance in the dataset, and since the eigenvector coefficients were all positive and of a similar magnitude, this axis can again be interpreted as representing size. PC-II accounted for 3.6% of the total variance, and compared with the eigenvector coefficients from the first PCA, the coefficients for each measurement in this case fell in relatively the same locations as in the previous analysis, simply with loadings for pedal phalanges being absent. The largest contrast on PC-II is thus between individuals with long manual phalanges and individuals with a long femur and ilium. It appears safe to assume that this axis can again be interpreted as separating more terrestrial taxa on the positive end from more aquatic taxa on the negative end. PC-III accounted for 0.9% of the total variance, and while the more intermediate eigenvector coefficients shifted around slightly, the most extreme values are the same as in the first PCA. The largest contrast on PC-III in this second case is between individuals with a long lumbus, long third metatarsal, and long tibia and individuals with a long third metacarpal and long manual phalanges. This axis can again be interpreted as separating hind limb-dominated

swimmers with more negative PC-III scores from forelimb-dominated swimmers with more positive PC-III scores. PC scores for each taxon for the first three principal components are listed in Table 4 and shown graphically in Figures 5-6. When PC scores are calculated for *Allodesmus* and plotted in the same space as the scores of the extant species, it plots among the larger pinnipeds but appears less aquatic than all pinnipeds except for *Odobenus*. On the locomotion axis, *Allodesmus* plots outside of both the Phocidae and the Otariidae, but is much closer to the Otariidae on the forelimb-dominated side of the axis. This implies that *Allodesmus* has skeletal proportions similar to pectoral oscillators and swam primarily using its forelimbs, which is counter to the most recent interpretations of locomotion in this species.

These new locomotor interpretations were then analyzed in a phylogenetic context following the approach of Berta and Adam (2001) (Figure 7). The topology of the tree follows the results of Berta and Wyss (1994) and Deméré (1994), and the inferred locomotor modes of taxa not included in the PCA follow the interpretations of Berta and Adam (2001). If *Enaliarctos* is indeed a hind limb-dominated swimmer and *Allodesmus* a forelimb-dominated swimmer as the PCA results suggest, then it appears that hind limb-dominated swimming had to have arisen at least two times independently. If we posit that hind limb swimming arose once at the base of the Phocomorpha ([Desmatophocidae + Phocidae] + Odobenidae) and once in the Enaliarctinae lineage, then we also must posit an additional reversal to forelimb swimming in the Desmatophocidae. Another possibility would be to propose that hind limb swimming arose independently within the Phocidae and the Odobenidae, which would decrease the number of reversals to forelimb swimming (only once within the Dusiagnathinae), but would increase the number of independent acquisitions of hind limb-dominated swimming to three. The main point is that if these locomotor interpretations are correct for *Enaliarctos* and *Allodesmus*, then the

evolution of swimming in pinnipeds involves a number of additional locomotor transitions than what Berta and Adam's (2001) initial analysis proposed.

Discussion

Like many other tetrapod groups, ancestral pinnipeds embarked on a journey beginning on land and eventually finishing in the sea. Looking at modern secondarily-aquatic vertebrates and their supposed ancestral groups, it is clear that the starting and ending points for each of these land-to-sea transitions are unique, and the pathway that each of these lineages took to readapt to an aquatic environment was novel as well (Gingerich 2005). One aspect of reconstructing and understanding these transitions is to elucidate the evolution of locomotor modes, which informs us about the way in which an organism could interact with other species in its environment.

Previous attempts to analyze the evolution of locomotion in pinnipeds have relied on the presence or absence of osteological characters associated with each swimming mode (Berta and Adam 2001). This technique may work well for taxa close to the modern groups of pinnipeds, but it presents difficulties when interpreting locomotor capabilities in taxa that are less closely-related to the modern clades. Both *Enaliarctos mealsi* (Berta et al. 1989; Berta and Ray 1990) and *Allodesmus kernensis* (Giffin 1992) had been described as possessing features consistent with using forelimbs, hind limbs, and their axial skeleton to generate thrust during aquatic locomotion, but were shoehorned into either forelimb- or hind limb-dominated swimming based on possession of a handful of characters (Berta and Adam 2001; Berta et al. 2006). Their relatively complete skeletons allow their overall skeletal proportions to be looked at in comparison with modern semiaquatic taxa, and by elucidating which modern taxa they are most

similar to proportionally, we have a way to quantitatively assess locomotor interpretations in these fossil taxa.

The placement of *Enaliarctos* on the size axis (PC-I) indicated that it was an average-sized species when compared with modern pinnipeds, and it appeared to be less aquatic than most of the modern pinnipeds on the axis for PC-II. It plotted among the phocids on the locomotion axis (PC-III), suggesting that it swam using a hind limb-dominated mode of locomotion. This interpretation is in contrast to recent suggestions that it was more specialized for forelimb swimming (Berta and Adam 2001; Berta et al. 2006), but given that its hind limbs are relatively larger than its forelimbs (Berta and Ray 1990), hind limb-dominated swimming seems like a more plausible interpretation. *Allodesmus* appeared to be of a similar size to some of the larger modern pinnipeds, but like *Enaliarctos*, its PC-II score indicated that it was less aquatically-adapted than most modern pinnipeds. Its PC-III score placed it closest to modern otariids, which suggests that it might have used predominantly forelimb swimming. This, again, is in contrast to the most recent interpretations (Berta and Adam 2001; Berta et al. 2006), but it supports the notions put forth by earlier authors that this animal was similar to modern otariids in habit (Mitchell 1966; Barnes 1972; Mitchell 1975).

Placing these new interpretations onto a phylogeny to assess the evolution of swimming mode in pinnipeds complicates the picture depicted by Berta and Adam (2001), as it calls for several additional transitions in locomotor mode than they proposed. But subscribing to this overall picture of locomotor evolution is contingent upon the inferred phylogenetic relationships being correct. While pinnipeds are generally agreed to be a monophyletic group derived from arctoid carnivores, the relationships among members within the group are still contentious. Traditionally, otariids and odobenids were allied within the Otarioidea (McLaren 1960; Barnes

1972; Mitchell 1975; Tedford 1976; Barnes 1989), but many recent analyses have placed the odobenids as the sister group to the Phocoidea (Desmatophocidae + Phocidae), forming the Phocomorpha (Wyss 1987; Berta et al. 1989; Wyss 1989; Berta and Ray 1990; Berta 1991; Berta and Wyss 1994; Deméré and Berta 2002; Berta et al. 2006). Molecular analyses have consistently suggested that odobenids are more closely related to otariids (Sarich 1969; Árnason et al. 1995; Lento et al. 1995; Flynn and Nedbal 1998; Davis et al. 2004; Flynn and Wesley-Hunt 2005; Árnason et al. 2006), but some authors argue that these results are due to long-branch attraction since the odobenid lineage appears to have split off early in the history of the group (Berta and Adam 2001; Berta et al. 2006). Using inferred locomotor mode like a character on a phylogenetic tree to interpret the evolution of locomotion is obviously contingent on the topology of that tree, so the picture of swimming evolution derived from this strategy could change drastically if the inferred relationships among the groups were to change. Thus, the interpretations of locomotor evolution across all pinniped lineages should be viewed with caution in light of the equivocal relationships among the different groups.

We should also be careful not to think that any animal must use exclusively one swimming mode. Modern otters use a variety of different swimming modes depending on what they are doing and where they are in the water (Fish 1994), and even the modern walrus, while using primarily pelvic oscillation, is known to use pectoral paddling as well when swimming at slow speeds (Gordon 1981). Given that *Enaliarctos* (Berta et al. 1989; Berta and Ray 1990) and *Allodesmus* (Giffin 1992; Berta and Adam 2001) have both been described as possessing adaptations for multiple swimming modes, we must not too quickly interpret them as using solely forelimb- or hind limb-dominated swimming, despite their placement on the locomotion axis in the PCA. The PCA simply demonstrated which modern animals were most similar in

proportions to these fossil taxa, and by association, we were able to infer something about their locomotion based on that of the modern taxa with which they clustered. For *Enaliarctos* in particular, it is actually quite attractive to hypothesize that it may have used multiple locomotor modes given its relationship to modern pinnipeds. If it could be shown to be the common ancestor of all later pinnipedimorphs rather than the outgroup to them, it may help explain how distinctly different locomotor modes (fore- and hind limb-dominated swimming) could have evolved from a common ancestor that showed a propensity for both fore- and hind limb swimming. By incorporating stratigraphic data into these phylogenetic reconstructions, we could test ancestor-descendent hypotheses, and this may offer a more complete picture of both locomotor evolution and the evolution of these groups in general.

The PCA performed in this paper was successful in demonstrating the modern pinnipeds to which *Enaliarctos mealsi* and *Allodesmus kernensis* were most similar in skeletal proportions. Their similarity to modern phocids and otariids respectively called into question some previous hypotheses of dominant swimming mode, thus slightly complicating our view of how this critical behavior evolved within the group. Yet while these results may obscure our understanding of the evolution of this behavior, they demonstrate the importance of using multiple approaches to assess behavior in extinct taxa. Using solely osteological characters or statistical techniques gives an incomplete picture of these animals and their supposed abilities. Interpretations from statistical analyses like the PCA performed here should be used to supplement an assessment of osteological characters when inferring locomotor modes and other behaviors, as it is important to garner as much information as possible when reconstructing the lifestyles of extinct creatures.

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Figures:

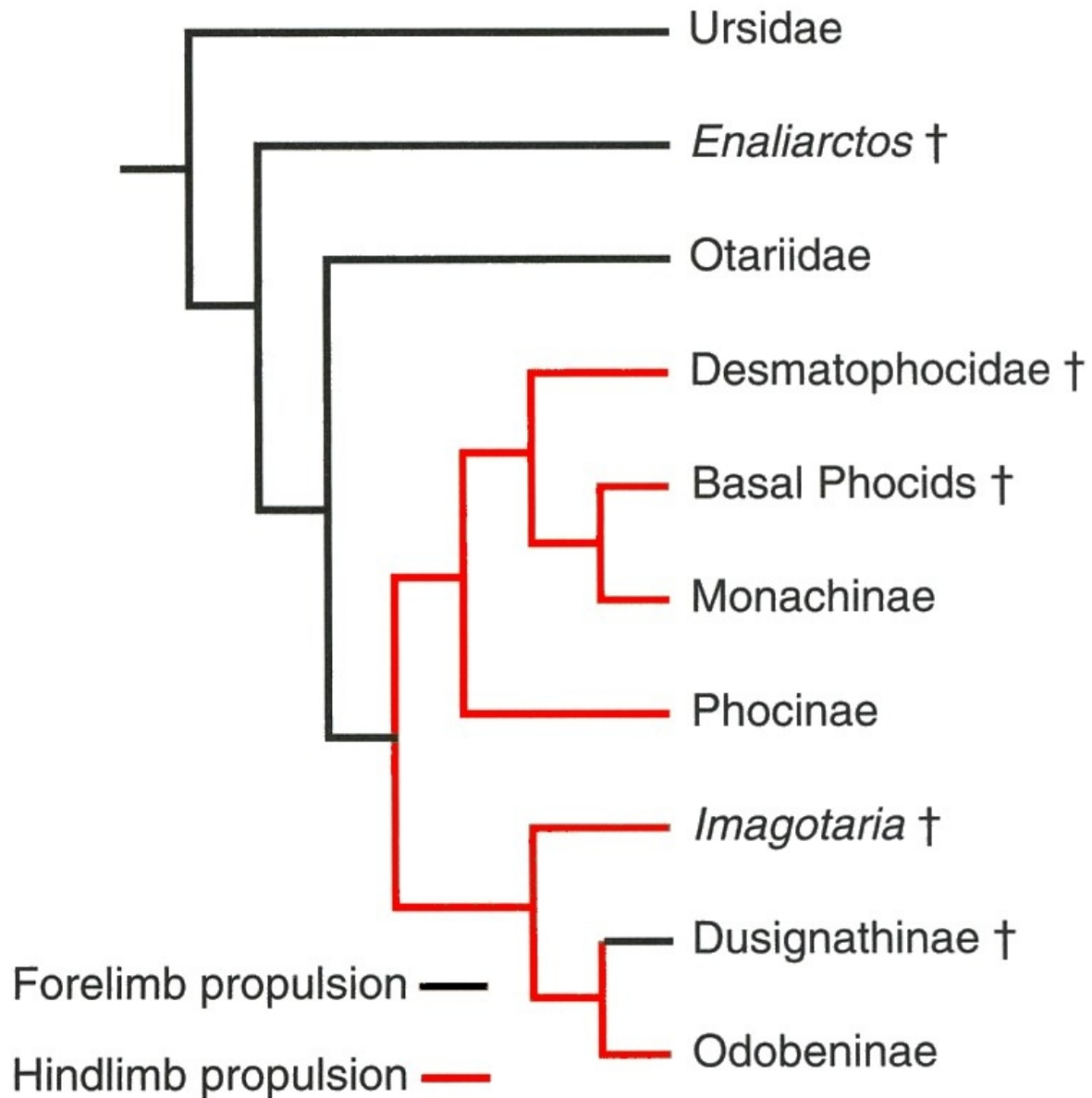


Figure 1. Modified from Berta et al. (2006). Phylogeny of pinnipeds showing proposed evolution of forelimb- and hind limb-dominated swimming.

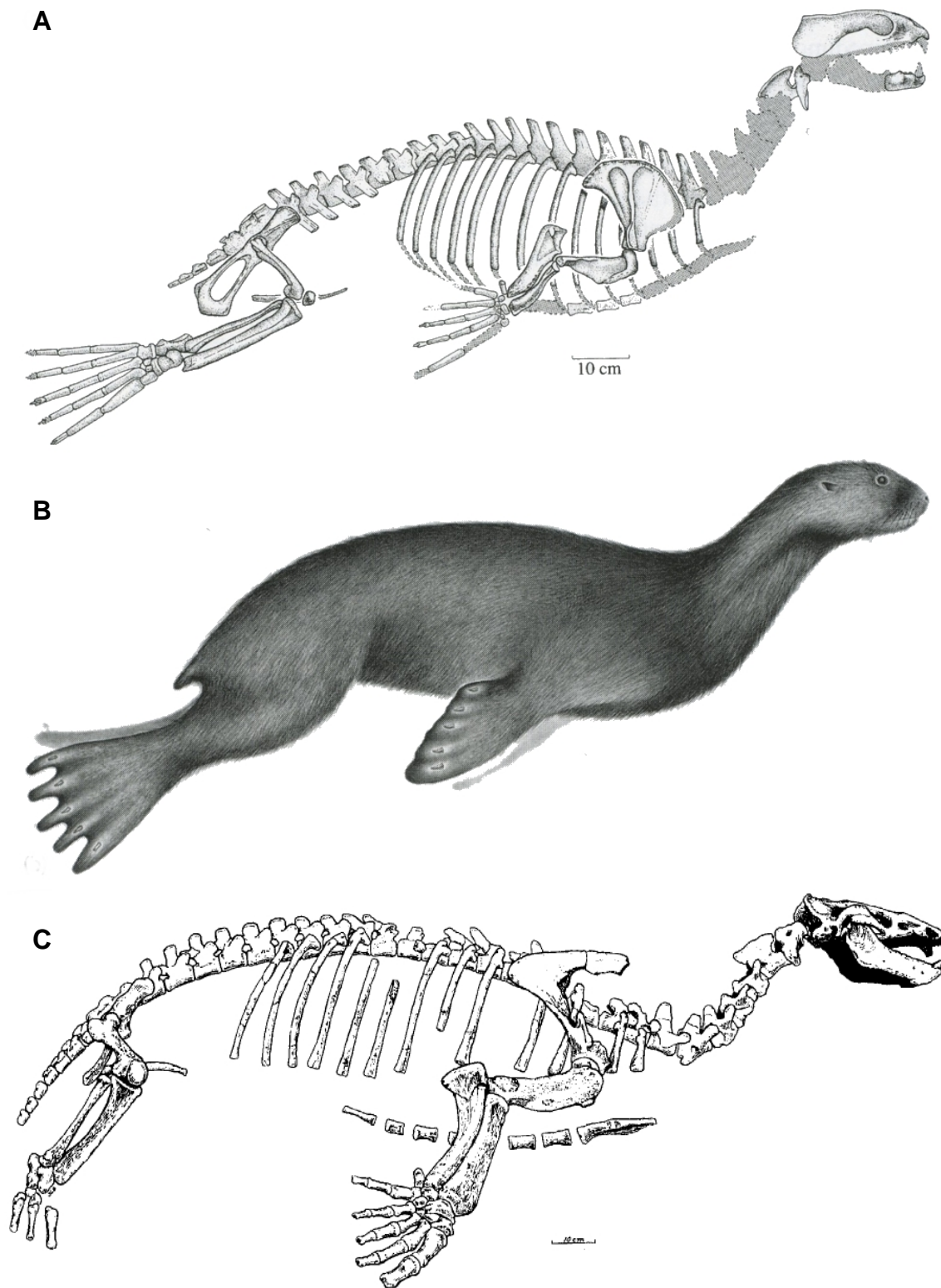


Figure 2. A.-B. Skeletal reconstruction and life restoration of *Enaliarctos mealsi* from Berta et al. (2006). Scale bar is 10 cm. **C.** Skeletal reconstruction of *Allodesmus kernensis* from Mitchell (1975). Scale bar is 10 cm.

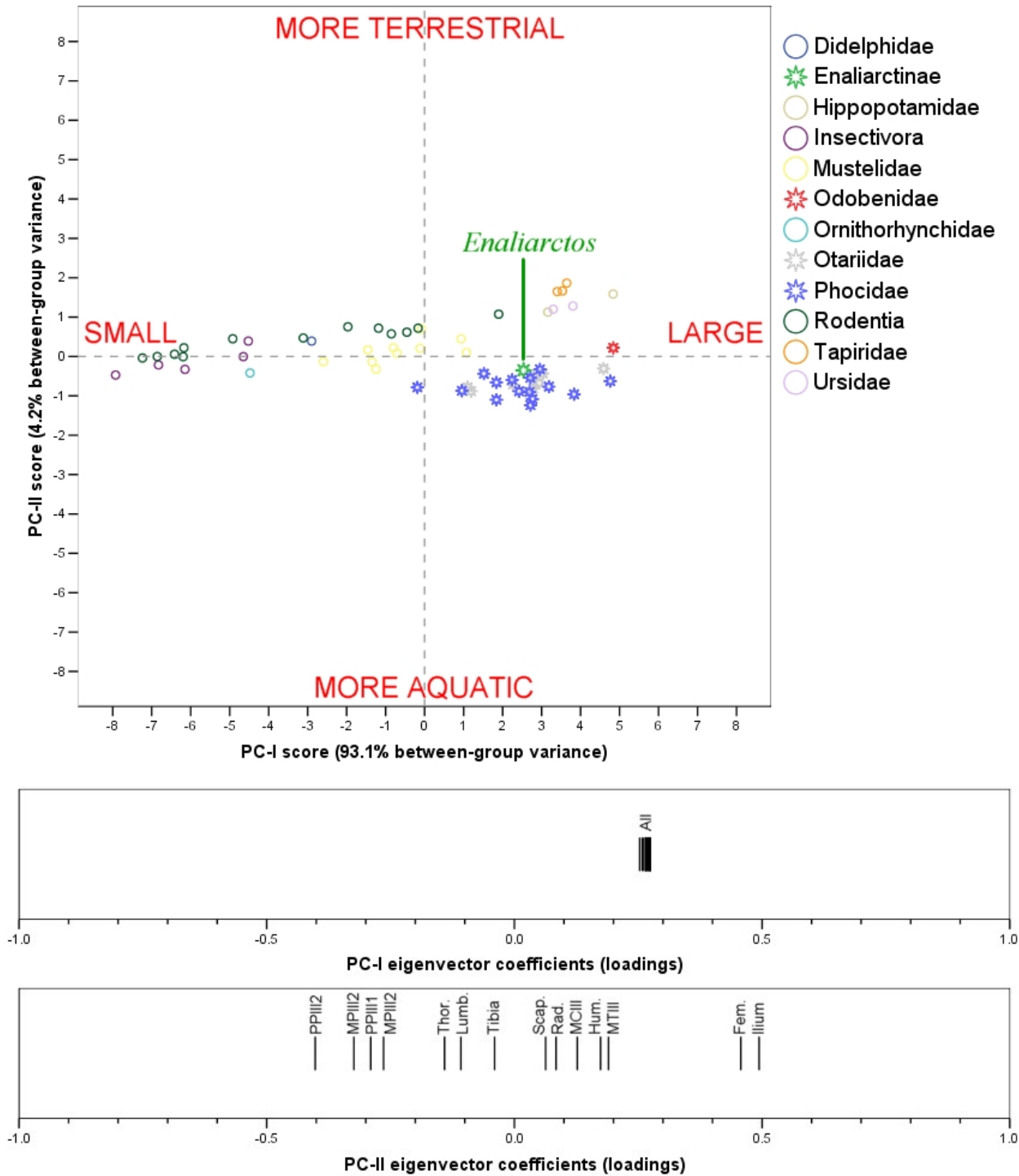


Figure 3. Results of PCA on 14 skeletal measurements of 61 extant semiaquatic mammals. PC-II scores are plotted against PC-I scores for each taxon. PC-I is interpreted as a size axis since all eigenvector coefficients are positive and of roughly equal magnitude. PC-II is interpreted as separating more aquatic species (with long manual and pedal phalanges) from more terrestrial species (with a long femur and a long ilium). *Enaliarctos* is average in size compared with other pinnipeds but is less aquatic than most otariids and phocids.

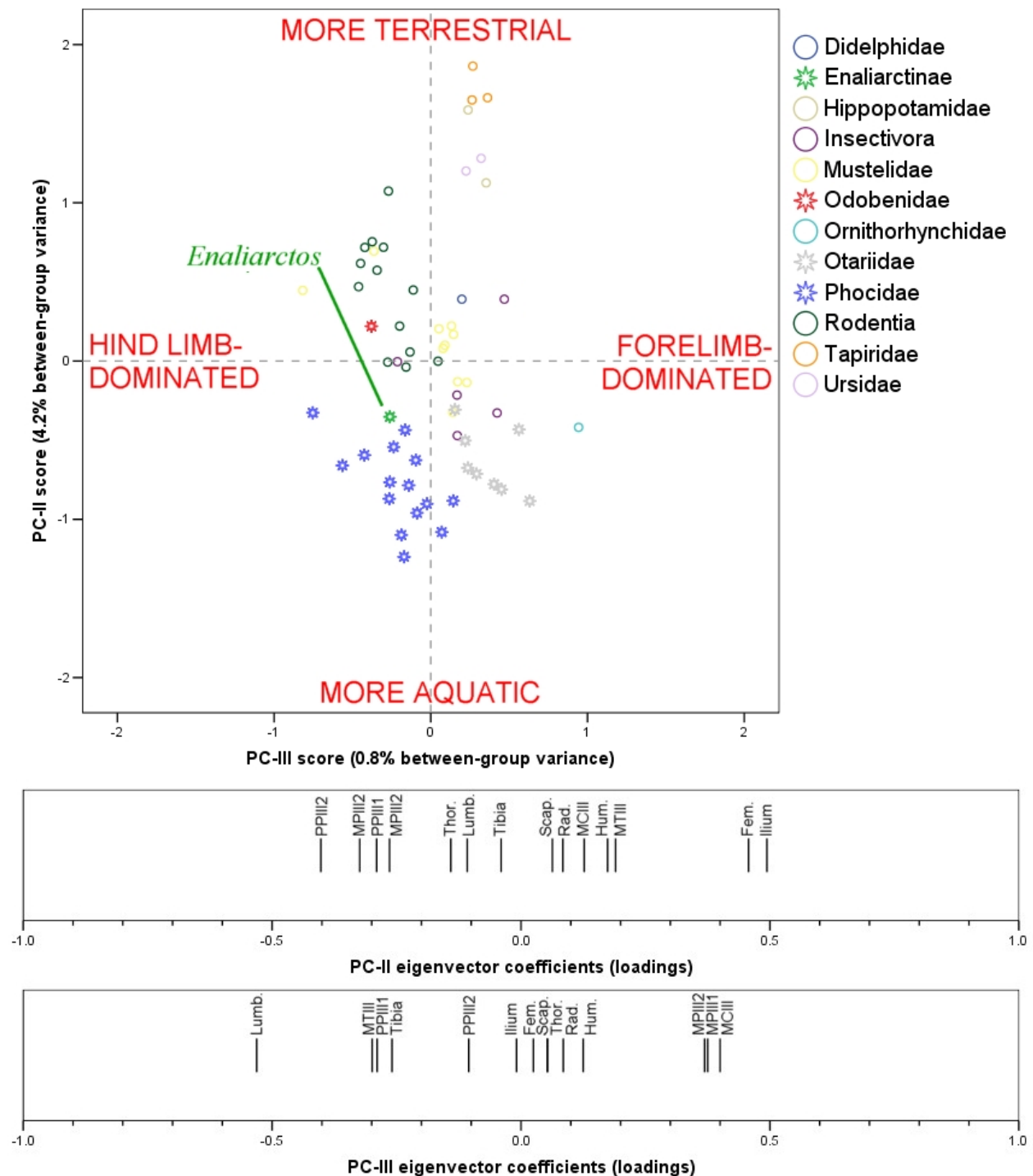


Figure 4. Results of PCA on 14 skeletal measurements of 61 extant semiaquatic mammals. PC-II scores are plotted against PC-III scores for each taxon. PC-II is interpreted as separating more aquatic species (with long manual and pedal phalanges) from more terrestrial species (with a long femur and long ilium). PC-III is interpreted as separating hind limb-dominated swimmers (with a long lumbus, a long third metatarsal, a long tibia, and long pedal phalanges) from forelimb-dominated swimmers (with a long third metacarpal and long manual phalanges). *Enaliarctos* plots with the phocids and is interpreted as being primarily a hind limb swimmer.

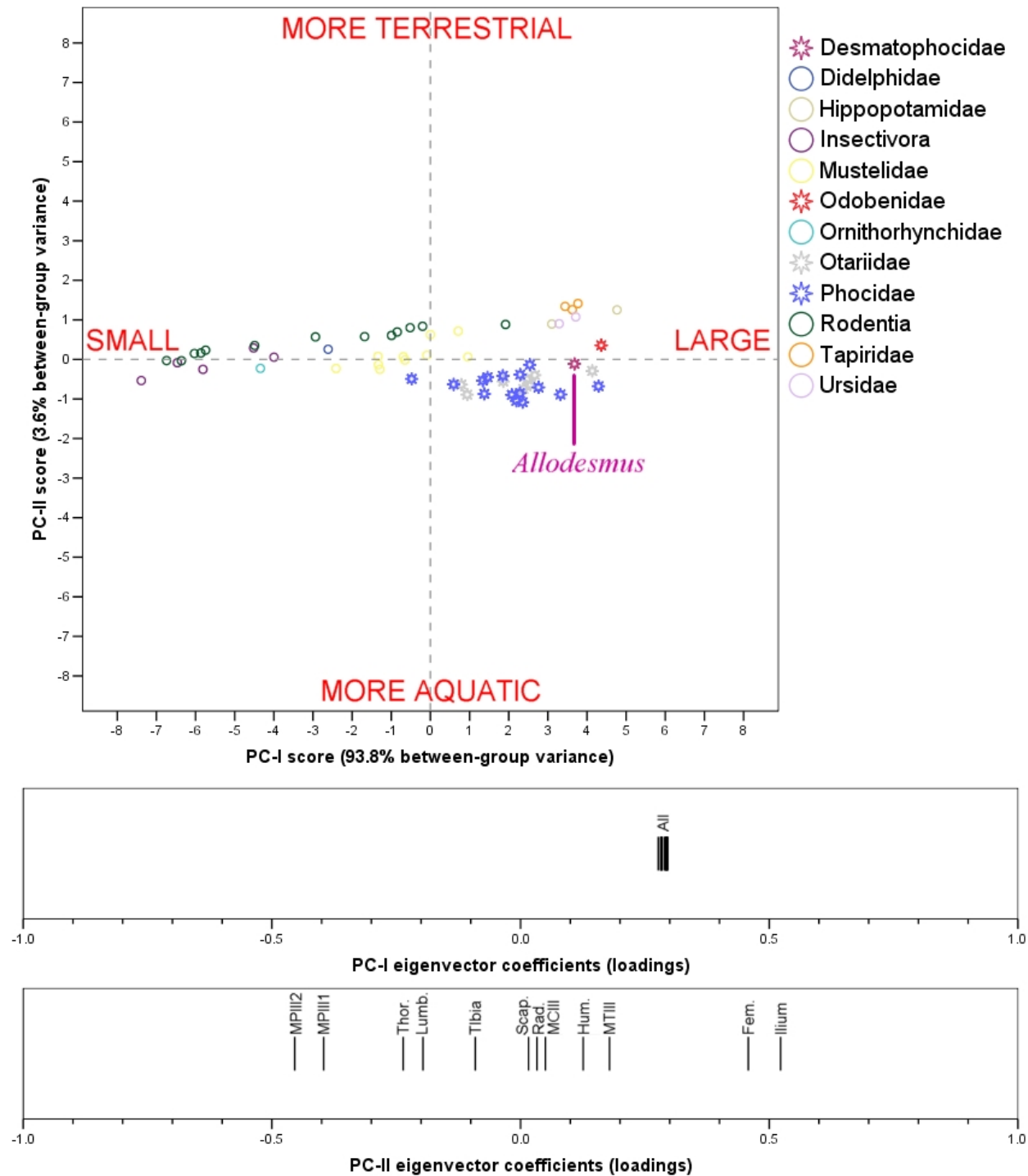


Figure 5. Results of PCA on 12 skeletal measurements of 61 extant semiaquatic mammals. PC-II scores are plotted against PC-I scores for each taxon. PC-I is interpreted as a size axis since all eigenvector coefficients are positive and of roughly equal magnitude. PC-II is interpreted as separating more aquatic species (with long manual phalanges) from more terrestrial species (with a long femur and a long ilium). *Allodesmus* is larger than most modern pinnipeds but is less aquatic than all modern pinnipeds except for *Odobenus*.

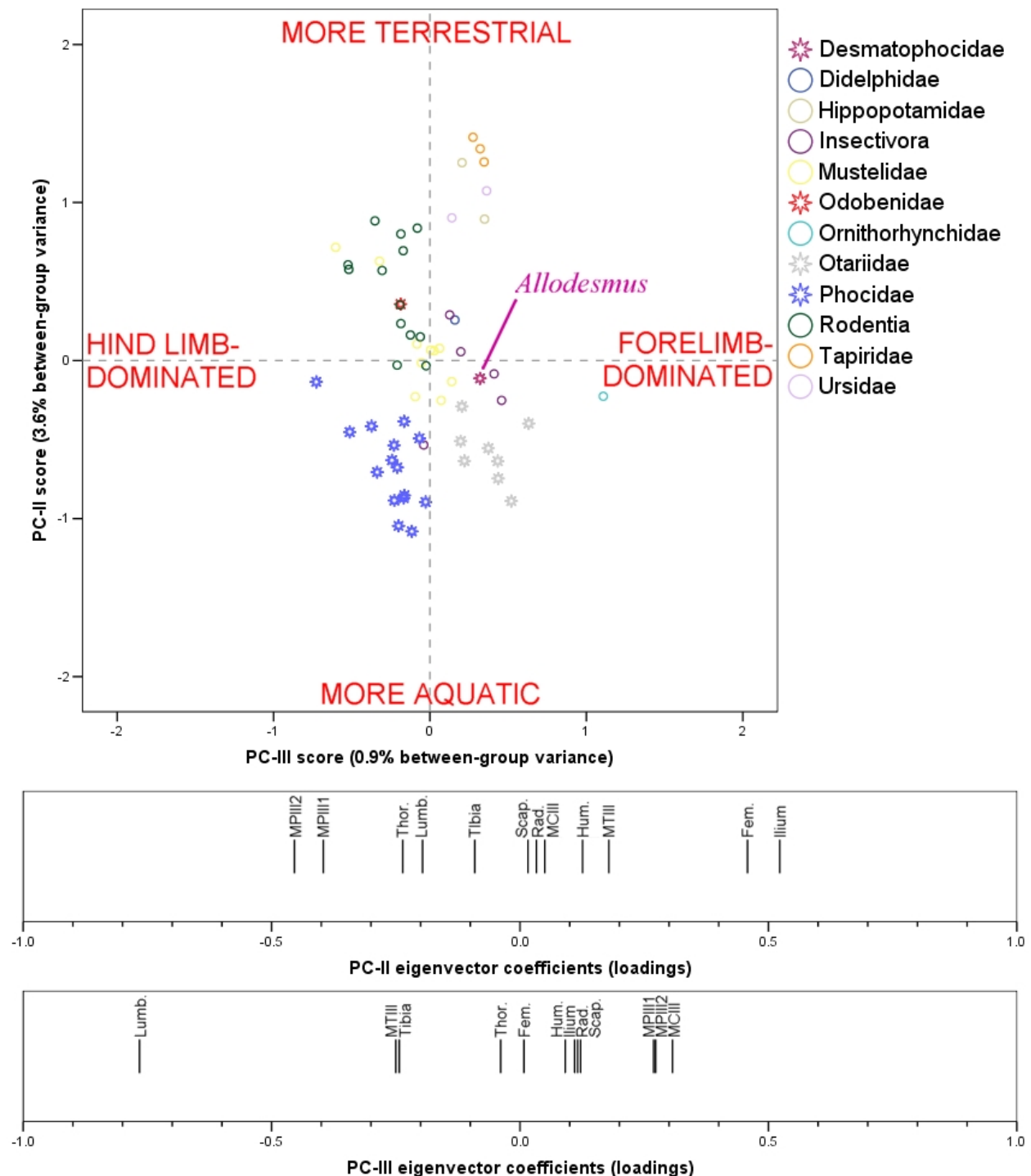


Figure 6. Results of PCA on 12 skeletal measurements of 61 extant semiaquatic mammals. PC-II scores are plotted against PC-III scores for each taxon. PC-II is interpreted as separating more aquatic species (with long manual phalanges) from more terrestrial species (with a long femur and long ilium). PC-III is interpreted as separating hind limb-dominated swimmers (with a long lumbus, a long third metatarsal, and a long tibia) from forelimb-dominated swimmers (with a long third metacarpal and long manual phalanges). *Allodesmus* plots near the otariids and is interpreted as being primarily a forelimb swimmer.

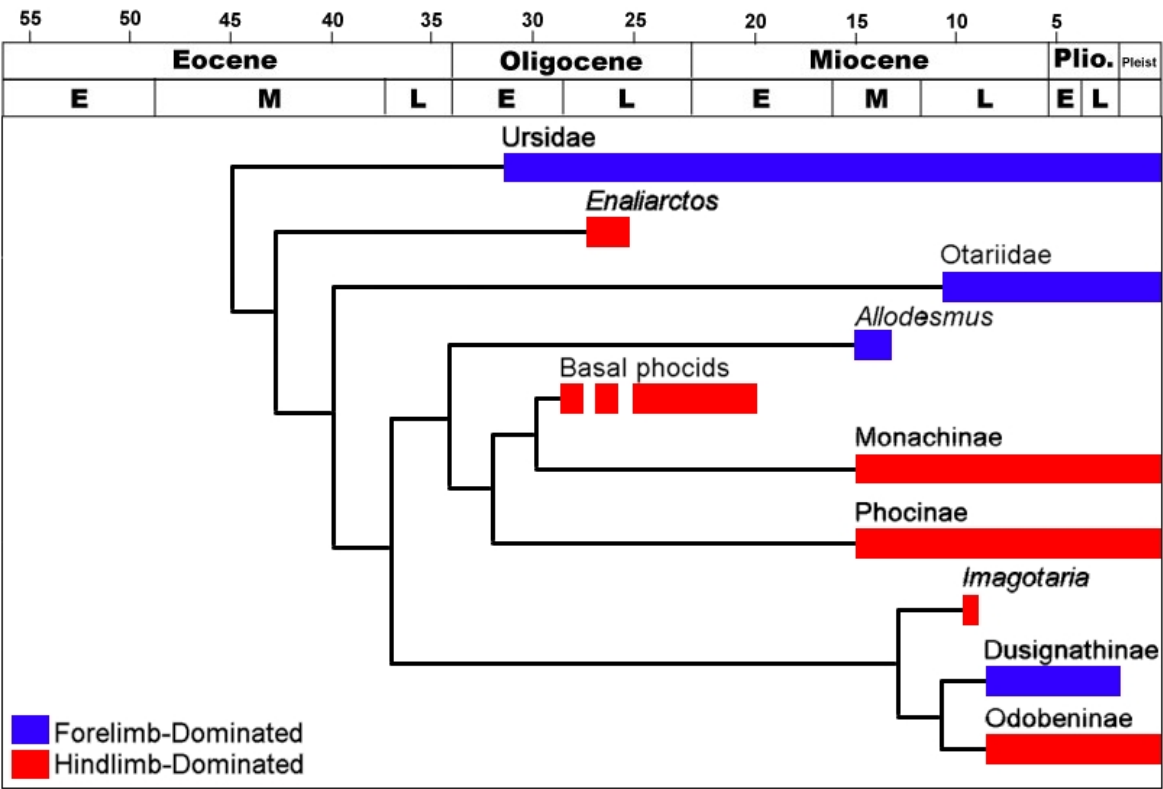


Figure 7. Phylogeny and stratigraphic ranges of pinnipeds following Berta and Wyss (1994) and Deméré (1994) showing the evolution of aquatic locomotion. Ranges marked with blue bars indicate forelimb-dominated swimmers, while red bars indicate hind limb-dominated swimmers.

Genus & Species	Family	Sex	Reference	Measurements (cm)													
				Thor	Lum	Scap	Hum	Rad	MCIII	MPIII1	MPIII2	Ilium	Fem	Tib	MTIII	PPIII1	PPIII2
<i>Arctocephalus galapagoensis</i>	Otariidae	F	AMNH 100319	38.30	12.50	11.67	10.31	11.09	4.32	3.05	2.66	5.69	6.60	13.10	4.17	4.06	3.73
<i>Neophoca cinerea</i>	Otariidae	--	USNM 504729	62.90	16.00	21.60	19.10	19.70	6.84	5.54	4.52	9.00	12.32	20.50	6.86	6.12	5.08
<i>Otaria flavescens</i>	Otariidae	--	AMNH 256447	35.00	13.10	10.45	9.81	9.71	4.59	5.26	3.18	5.11	7.28	12.41	4.90	3.64	3.39
<i>Zalophus wolfebaeki</i>	Otariidae	M	AMNH 63946	66.30	23.00	20.60	16.50	17.70	5.71	4.68	3.91	8.58	10.90	21.20	6.22	5.59	4.53
<i>Monachus schauinslandi</i>	Phocidae	F	USNM 243839	76.20	35.50	14.15	13.48	13.60	6.06	6.17	4.67	6.37	10.09	20.60	5.94	7.00	4.69
<i>Monachus tropicalis</i>	Phocidae	M	AMNH 77741	66.50	29.00	13.40	14.95	13.60	4.74	4.84	4.42	6.78	10.25	20.00	4.93	5.43	4.45
<i>Pusa caspica</i>	Phocidae	M	USNM 341615	37.20	16.50	10.20	8.50	8.78	4.01	2.60	1.59	3.89	7.32	18.70	5.07	4.50	3.87
<i>Pusa hispida</i>	Phocidae	--	AMNH 75250	23.00	10.90	8.29	7.39	5.91	2.53	1.64	1.56	3.48	6.36	12.30	3.77	3.29	3.00
<i>Aonyx capensis</i>	Mustelidae	F	AMNH 51853	26.50	12.00	8.96	11.26	9.24	1.57	1.48	0.78	6.97	11.63	11.32	4.55	2.05	1.29
<i>Hydricitis maculicollis</i>	Mustelidae	F	AMNH 51825	19.00	8.50	4.41	6.28	4.39	2.08	1.55	1.18	3.81	6.16	6.98	3.38	2.03	1.45
<i>Lontra longicaudis</i>	Mustelidae	F	AMNH 205902	23.00	10.10	6.36	7.91	5.52	2.47	1.52	1.02	4.93	7.64	8.29	3.64	1.78	1.04
<i>Enaliarctos mealsi</i>	Enaliarctidae	--	USNM 374272	4.05	3.37	2.73	2.69	2.46	1.75	1.40	1.01	1.87	2.62	3.14	2.18	1.65	1.42
<i>Allodesmus kernensis</i>	Desmatophocidae	--	LACM 4320	4.45	3.35	3.22	3.31	3.24	2.12	1.94	1.51	2.63	2.88	3.26	2.10	--	--

Table 1. Skeletal measurements of the 11 additional extant semiaquatic taxa included in this analysis in addition to the 50 species from Gingerich (2003), as well as measurements of the fossil pinnipedimorphs *Enaliarctos mealsi* and *Allodesmus kernensis*. Abbreviations: AMNH, American Museum of Natural History, New York, NY; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA; USNM, United States National Museum, Washington, DC.

PC	Eigenvalue	Eigenvector Coefficients (Loadings)													
		Thor	Lum	Scap	Hum	Rad	MCIII	MPIII1	MPIII2	Ilium	Fem	Tib	MTIII	PPIII1	PPIII2
I	13.040	0.272	0.265	0.274	0.273	0.274	0.270	0.267	0.265	0.253	0.258	0.274	0.269	0.266	0.261
II	0.589	-0.141	-0.108	0.063	0.174	0.084	0.127	-0.264	-0.324	0.494	0.457	-0.040	0.190	-0.290	-0.402
III	0.117	-0.053	0.531	-0.053	-0.125	-0.085	-0.400	-0.375	-0.369	0.009	-0.025	0.259	0.299	0.289	0.105
IV	0.084	0.147	0.687	-0.311	0.071	-0.186	0.239	0.145	0.094	-0.218	0.164	-0.141	-0.094	-0.340	-0.255
V	0.044	-0.299	-0.051	-0.239	-0.215	-0.239	0.264	0.183	0.131	0.115	-0.148	-0.322	0.677	0.175	-0.005
VI	0.032	0.400	0.040	-0.028	-0.012	-0.409	-0.355	0.147	0.068	0.567	0.009	-0.361	-0.200	0.159	0.024
VII	0.025	-0.153	-0.128	-0.540	0.259	0.049	-0.175	-0.227	0.229	-0.060	0.457	-0.123	-0.026	-0.008	0.486
VIII	0.023	-0.542	0.211	-0.094	-0.020	0.393	-0.361	0.329	0.250	0.213	-0.021	0.009	-0.197	0.146	-0.301
IX	0.017	-0.178	0.019	-0.189	-0.475	-0.183	0.456	-0.029	-0.080	0.248	0.188	0.318	-0.427	0.252	0.115
X	0.012	-0.266	0.303	0.304	0.056	0.111	0.225	-0.413	0.150	0.246	-0.330	-0.361	-0.170	-0.189	0.348
XI	0.008	-0.428	0.040	0.499	0.201	-0.534	-0.078	0.194	-0.044	-0.235	0.343	-0.043	-0.072	0.075	0.093
XII	0.004	-0.036	0.060	-0.062	-0.053	0.266	0.018	0.483	-0.666	0.018	0.023	-0.255	-0.045	-0.137	0.393
XIII	0.004	-0.009	0.003	0.130	-0.469	-0.072	-0.265	0.130	0.243	0.138	0.102	0.288	0.191	-0.635	0.244
XIV	0.002	0.168	0.040	0.257	-0.518	0.296	-0.046	-0.152	0.101	-0.251	0.439	-0.453	0.016	0.206	-0.094
61-sp. mean		3.203	2.478	2.132	2.137	2.032	1.019	0.658	0.251	1.746	2.109	2.458	1.418	0.961	0.542
61-sp. st. dev.		1.176	1.007	0.995	0.944	0.927	0.985	1.019	1.125	0.822	0.869	0.841	0.744	0.971	1.111

Table 2. Eigenvalues and eigenvector coefficients (loadings) for each principal component based on a PCA of 14 skeletal measurements of 61 extant semiaquatic mammals. Principal component scores for additional taxa could be calculated by normalizing the natural log-transformed measurements (subtract the 61-species mean from the natural log-transformed measurement, and divide that difference by the 61-species standard deviation), multiplying them by the appropriate eigenvector coefficients, and summing these products across all measurements.

PC	Eigenvalue	Eigenvector Coefficients (Loadings)											
		Thor	Lum	Scap	Hum	Rad	MCIII	MPIII1	MPIII2	Ilium	Fem	Tib	MTIII
I	11.255	0.291	0.284	0.295	0.295	0.295	0.292	0.285	0.282	0.277	0.282	0.293	0.290
II	0.435	-0.236	-0.196	0.016	0.126	0.033	0.050	-0.396	-0.454	0.523	0.458	-0.091	0.179
III	0.109	0.039	0.766	-0.122	-0.091	-0.116	-0.307	-0.269	-0.273	-0.110	-0.008	0.243	0.250
IV	0.059	-0.009	0.334	-0.481	0.071	-0.320	0.432	0.154	0.113	-0.011	0.317	-0.464	-0.102
V	0.041	-0.332	-0.103	-0.060	-0.239	-0.080	0.193	0.133	0.095	0.001	-0.293	-0.118	0.805
VI	0.031	0.417	0.018	0.130	-0.082	-0.398	-0.388	0.183	0.056	0.560	-0.199	-0.317	0.056
VII	0.023	-0.476	0.111	-0.286	0.141	0.355	-0.541	0.196	0.369	0.200	0.113	-0.105	-0.047
VIII	0.018	-0.395	0.299	0.234	-0.451	0.047	0.301	0.178	-0.103	0.389	-0.215	0.121	-0.386
IX	0.012	0.155	-0.259	-0.468	-0.438	-0.172	-0.058	0.180	0.067	0.136	0.298	0.567	0.017
X	0.008	0.253	0.027	-0.327	-0.108	0.323	0.205	-0.599	0.355	0.271	-0.331	-0.032	-0.035
XI	0.006	-0.278	0.004	0.323	0.042	-0.536	-0.020	-0.380	0.564	-0.021	0.181	0.176	-0.038
XII	0.002	0.162	0.046	0.283	-0.626	0.284	-0.117	-0.095	0.138	-0.201	0.441	-0.371	0.070
61-sp. mean		3.209	2.478	2.140	2.147	2.045	1.025	0.667	0.259	1.759	2.113	2.460	1.417
61-sp. st. dev.		1.181	1.007	1.002	0.954	0.938	0.991	1.028	1.132	0.830	0.872	0.842	0.742

Table 3. Eigenvalues and eigenvector coefficients (loadings) for each principal component based on a PCA of 12 skeletal measurements of 61 extant semiaquatic mammals. Principal component scores for additional taxa could be calculated by normalizing the natural log-transformed measurements (subtract the 61-species mean from the natural log-transformed measurement, and divide that difference by the 61-species standard deviation), multiplying them by the appropriate eigenvector coefficients, and summing these products across all measurements.

Species	14 measurements			12 measurements		
	PC-I	PC-II	PC-III	PC-I	PC-II	PC-III
<i>Ornithorhynchus anatinus</i>	-4.537	-0.418	-0.944	-4.343	-0.226	-1.108
<i>Chironectes minimus</i>	-2.951	0.396	-0.201	-2.613	0.257	-0.159
<i>Potamogale velox</i>	-4.582	0.395	-0.470	-3.997	0.056	-0.197
<i>Limnogale mergulus</i>	-6.214	-0.328	-0.423	-5.811	-0.252	-0.458
<i>Neomys fodiens</i>	-8.001	-0.473	-0.166	-7.387	-0.534	0.040
<i>Desmana moschata</i>	-4.711	-0.001	0.214	-4.517	0.289	-0.126
<i>Galemys pyrenaicus</i>	-6.896	-0.215	-0.165	-6.466	-0.084	-0.410
<i>Ursus americanus</i>	3.272	1.216	-0.233	3.290	0.903	-0.140
<i>Ursus maritimus</i>	3.778	1.296	-0.330	3.712	1.074	-0.362
<i>Mustela vison</i>	-2.649	-0.127	-0.173	-2.412	-0.229	0.094
<i>Lutra lutra</i>	-0.160	0.210	-0.057	-0.090	0.104	0.083
<i>Lontra canadensis</i>	-0.752	0.085	-0.082	-0.652	-0.014	0.055
<i>Lontra felina</i>	-1.395	-0.132	-0.234	-1.328	-0.133	-0.139
<i>Pteronura brasiliensis</i>	1.034	0.108	-0.096	0.957	0.062	-0.027
<i>Aonyx cinereus</i>	-1.503	0.174	-0.149	-1.341	0.077	-0.061
<i>Enhydra lutris</i>	0.892	0.456	0.814	0.711	0.716	0.603
<i>Callorhinus ursinus</i>	2.751	-0.807	-0.459	2.375	-0.746	-0.436
<i>Arctocephalus australis</i>	2.230	-0.709	-0.299	1.859	-0.555	-0.373
<i>Zalophus californianus</i>	2.909	-0.671	-0.244	2.552	-0.635	-0.220
<i>Eumetopias jubatus</i>	4.567	-0.299	-0.163	4.134	-0.290	-0.204
<i>Odobenus rosmarus</i>	4.817	0.231	0.372	4.363	0.357	0.188
<i>Monachus monachus</i>	2.657	-0.898	0.018	2.285	-0.853	0.164
<i>Lobodon carcinophagus</i>	1.806	-1.097	0.182	1.376	-0.870	0.168
<i>Hydrurga leptonyx</i>	3.806	-0.956	0.080	3.323	-0.885	0.228
<i>Leptonychotes weddelli</i>	3.156	-0.761	0.255	2.760	-0.706	0.338
<i>Ommatophoca rossii</i>	2.683	-1.236	0.165	2.195	-1.046	0.201
<i>Mirounga leonina</i>	4.739	-0.620	0.088	4.293	-0.676	0.209
<i>Erignathus barbatus</i>	2.926	-0.321	0.748	2.539	-0.135	0.727
<i>Cystophora cristata</i>	2.681	-0.538	0.232	2.293	-0.385	0.165
<i>Halichoerus grypus</i>	2.209	-0.589	0.419	1.850	-0.415	0.374
<i>Pagophilus groenlandicus</i>	1.805	-0.656	0.560	1.457	-0.452	0.513
<i>Phoca vitulina</i>	1.484	-0.431	0.158	1.337	-0.536	0.230
<i>Tapirus terrestris</i>	3.507	1.680	-0.371	3.625	1.257	-0.346
<i>Tapirus bairdii</i>	3.374	1.666	-0.272	3.440	1.340	-0.321
<i>Tapirus indicus</i>	3.619	1.881	-0.277	3.768	1.413	-0.275
<i>Hippopotamus amphibius</i>	4.814	1.604	-0.247	4.766	1.252	-0.205
<i>Hexaprotodon liberiensis</i>	3.133	1.140	-0.361	3.101	0.895	-0.349
<i>Castor fiber</i>	-0.210	0.728	0.299	-0.201	0.838	0.081
<i>Castor canadensis</i>	-0.499	0.626	0.446	-0.519	0.801	0.186
<i>Neusticomys monticolus</i>	-7.310	-0.038	0.161	-6.741	-0.029	0.210
<i>Ichthyomys hydrobates</i>	-6.483	0.058	0.135	-6.030	0.150	0.062
<i>Ichthyomys tweedii</i>	-6.242	0.224	0.201	-5.744	0.234	0.186
<i>Rheomys raptor</i>	-6.927	-0.001	-0.044	-6.362	-0.033	0.025
<i>Rheomys underwoodi</i>	-6.261	-0.006	0.277	-5.865	0.162	0.125
<i>Arvicola terrestris</i>	-4.983	0.454	0.113	-4.490	0.352	0.191
<i>Ondatra zibethicus</i>	-3.168	0.476	0.461	-2.938	0.570	0.306
<i>Hydrochaeris hydrochaeris</i>	1.865	1.087	0.265	1.919	0.884	0.352
<i>Myocastor coypus</i>	-0.899	0.582	0.341	-0.849	0.695	0.171
<i>Sylvilagus aquaticus</i>	-1.230	0.726	0.418	-0.995	0.606	0.524
<i>Sylvilagus palustris</i>	-2.019	0.761	0.373	-1.682	0.577	0.519
<i>Arctocephalus galapagoensis</i>	1.065	-0.775	-0.409	0.788	-0.636	-0.433
<i>Neophoca cinerea</i>	3.001	-0.426	-0.571	2.665	-0.398	-0.631
<i>Otaria flavescens</i>	1.153	-0.882	-0.638	0.938	-0.889	-0.520
<i>Zalophus wolfebaeki</i>	2.764	-0.498	-0.227	2.467	-0.510	-0.196
<i>Monachus schauinslandi</i>	2.734	-1.079	-0.077	2.355	-1.081	0.116
<i>Monachus tropicalis</i>	2.390	-0.880	-0.150	2.079	-0.895	0.028
<i>Pusa caspica</i>	0.914	-0.869	0.260	0.592	-0.631	0.243
<i>Pusa hispida</i>	-0.230	-0.784	0.138	-0.480	-0.492	0.068
<i>Aonyx capensis</i>	-0.119	0.704	0.360	-0.001	0.629	0.323
<i>Hydricitis maculicollis</i>	-1.294	-0.321	-0.144	-1.294	-0.252	-0.072
<i>Lontra longicaudis</i>	-0.848	0.228	-0.136	-0.692	0.067	-0.004
<i>Enaliarctos mealsi</i>	2.537	-0.352	0.261	--	--	--
<i>Allodesmus kernensis</i>	--	--	--	3.679	-0.113	-0.320

Table 4. Principal components scores by species for PC-I, PC-II, and PC-III for both PCAs.