

Characterizing the Aquatic Locomotor Evolution of Archaeocetes Utilizing Post-Cranial
Geometric Morphometrics

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by

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DEDICATION

This is dedicated to my wonderful family, including my mother, Sally, my father, Robert, my sister, Rebekah, and my dog Mabel, and to my loving fiancée Giselle.

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LIST OF ABBREVIATIONS

Cairo Geological Museum	CGM
Geological Survey of Pakistan, University of Michigan collections	GSP-UM
Geological Survey of Pakistan, Howard University collections	H-GSP
Principal Components Analysis	PCA
University of Michigan Museum of Paleontology	UMMP
University of Michigan Museum of Zoology	UMMZ
U.S. National Museum of Natural History	USNM

ABSTRACT

CHARACTERIZING THE AQUATIC LOCOMOTOR EVOLUTION OF ARCHAEOCETES UTILIZING POST-CRANIAL GEOMETRIC MORPHOMETRICS

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Cetaceans are one of the most unusual and divergent forms of mammals in terms of both their morphology and ecology (Uhen, 2010). Numerous methods have been used to characterize the locomotion and locomotor evolution of cetaceans, from comparing fossil morphology to modern mammalian analogues (Thewissen and Fish, 1997) to observing the microstructure and osteology of archaeocete postcrania (Houssaye et al., 2015). I used three-dimensional landmark-based geometric morphometrics to analyze and compare the shape of archaeocete innominata and to investigate the controls on their morphology. While I had hypothesized that the shape of the innominate was primarily driven by aquatic locomotory mode, my results indicated that neither locomotory mode, nor the secondary factors of phylogenetic affinity and robustness fully explained the shape variability. This suggests that more of the postcranial skeleton, such as the hindlimb and vertebral column, must be looked at in conjunction to comprehend the drivers of innominate shape change.

INTRODUCTION

Cetaceans are one of the most unusual and divergent forms of mammals in terms of both their morphology and ecology (Uhen, 2010). All modern whales are obligately aquatic, with highly specialized aquatic adaptations, including a lack of hair and hindlimbs, flippers, tail flukes, a fusiform body, and cranial telescoping (Thewissen et al., 2001b). The most basal cetaceans, archaeocetes represent the transition from the terrestrial lifestyle of land-dwelling artiodactyls to the fully aquatic one of modern cetaceans (Bebej et al., 2012). When cetaceans transitioned from a fully terrestrial to a semi to fully aquatic niche, it involved drastic changes to morphology and physiology to become specialized in their aquatic ecology (Houssaye et al., 2015). These morphological and physiological changes, particularly of the innominate, hindlimb, and lumbocaudal region, tend to represent adaptations related to locomotion (Martín-Serra et al., 2014). One of the key aspects of mammalian biology is locomotion, because it reflects behaviors, especially hunting and foraging for food, escaping from predators, and migrating to new locations (Martín-Serra et al., 2014). Numerous methods have been used to characterize the locomotion and locomotor evolution of cetaceans, from comparing fossil morphology to modern mammalian analogues (Thewissen and Fish, 1997) to observing the microstructure and osteology of archaeocete postcrania (Houssaye et al., 2015). I made use of three-dimensional landmark-based geometric morphometrics to analyze and

compare the shape of archaeocete innominata and to investigate the controls on their morphology.

Mammalian & Cetacean Postcranial Anatomy

Central to the discussion of the aquatic locomotion of archaeocetes is their postcranial anatomy. It is with the analysis and understanding of postcranial anatomy that the phylogeny and style of aquatic locomotion can be recognized (Jones et al., 2019). It is of vital importance that phylogeny of archaeocetes be better understood, so that the overall evolutionary history of cetaceans may be characterized. Both the axial (including the skull, rib cage, and vertebral column) and appendicular (including shoulder and pelvic girdles and limb bones) skeleton are important as sources of propulsion and surfaces for that force to be dissipated into the fluid medium.

Anatomy and Function of the Axial Skeleton

The mammalian vertebral column normally consists of a variety of irregular bones, called vertebrae, though their overall number varies across mammalian taxa. The vertebral column consists of five types of vertebrae: cervical, thoracic, lumbar, sacral, and caudal (Evans et al., 2020). One of the main functions of the vertebral column is to protect and support the body. For many terrestrial and semi-aquatic mammals, it can also act as a flexible, slightly compressible rod through which the propelling force generated by the pelvic limbs is transmitted to the rest of the body. The vertebral column is also involved in the use of axial and abdominal muscles for locomotion. There is a huge range of mobility in terrestrial mammals. Most non-basilosaurid archaeocetes, similar to many terrestrial artiodactyls, maintained similar vertebral counts for each group, with 7

cervicals, 13 thoracics, 6 lumbar, ~3-4 sacral, and 21 caudal (Uhen, 2014). The anteriormost vertebrae are the cervicals, which support the head and muscles of the neck. The first two cervical vertebrae, the atlas and axis respectively, directly support the base of the skull and are easily distinguished from the rest of the cervicals (Evans et al., 2020). The mammalian vertebral column generally shows variability in count number, the cervical count of seven is mostly conserved (Asher et al., 2011). The thoracic vertebrae support the ribs, which protect vital internal organs, and the upper back. This is the least mobile segment in most mammals, and isn't as involved in locomotion (Evans et al., 2020). The lumbar, sacral and caudal vertebrae, being the posteriormost segments of the vertebral column, have the most control over locomotor propulsion (Buchholtz, 2001). The lumbar vertebrae support much of the trunk and help to provide flexibility for locomotion (Evans et al., 2020). The lumbar vertebrae of basal, terrestrial to semiaquatic archaeocetes are most similar to those of other terrestrial, dorsostable artiodactyls, while those of the more derived basilosaurid archaeocetes are most similar to dorsomobile mammals (Bebej and Smith, 2018). In most mammals, the sacral vertebrae are fused together to form the sacrum (Evans et al., 2020). The sacrum supports and stabilizes the trunk of terrestrial artiodactyls (Galis et al., 2014) and provides a mechanism for the aquatic locomotion of basal archaeocetes (Gol'din, 2014). As archaeocetes adapted to their marine lifestyle, they attained derived characters such as an increased lumbar count, but reduced sacral (Buchholtz, 2007). These sacral unfused and disarticulated from the innominate, becoming incorporated into the lumbocaudal region of the vertebral column (Uhen, 2014). The posteriormost vertebrae are the caudal (Evans et al., 2020). While we

tend to think of the vertebral column of terrestrial mammals as being separated into the aforementioned groups, it is possible that the vertebral column of artiodactyls may be further defined into larger precaudal and caudal modular groups (Buchholtz, 2007).

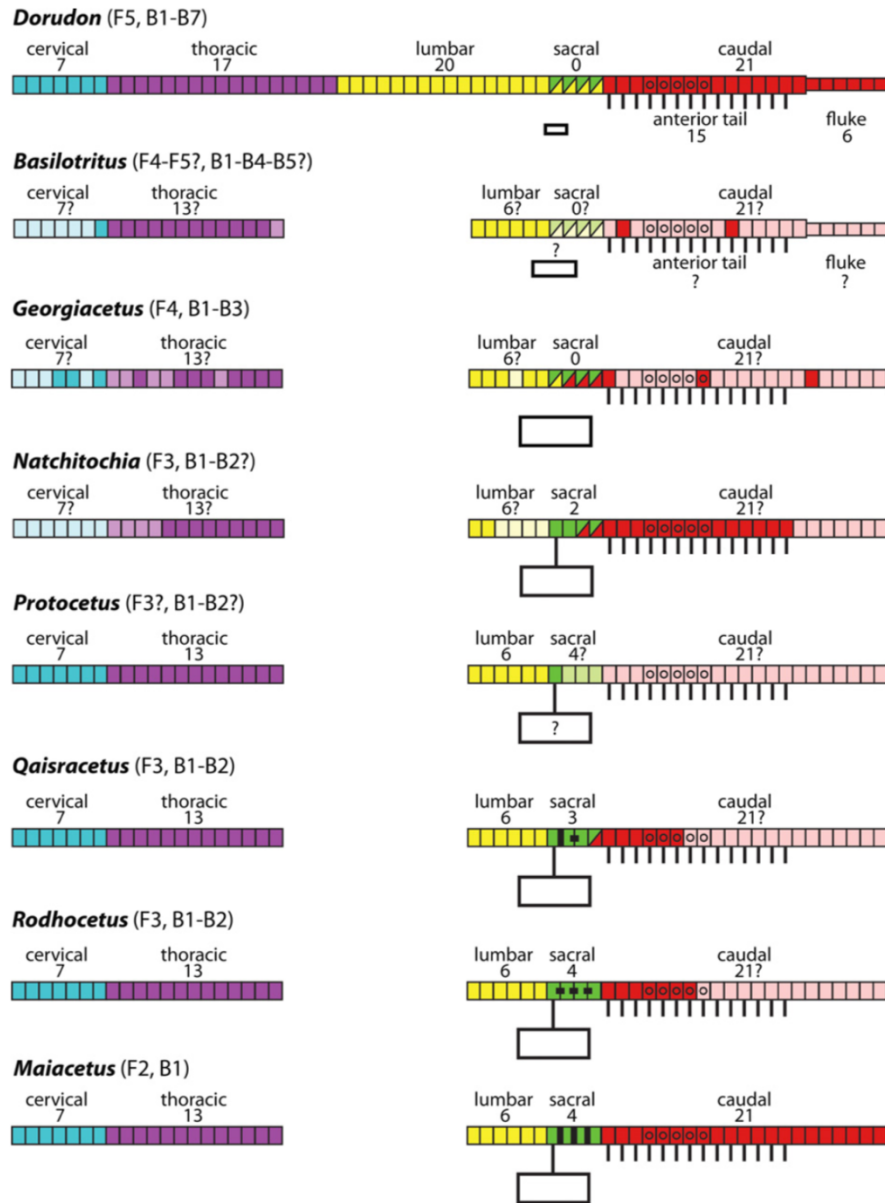


Figure 1 Schematic illustrations of the vertebral columns and counts of archaeocete taxa. Each vertebral group is assigned a color and labeled. The innominata are illustrated as white rectangles, some of which lack contact with the sacrum. Each F# refers to a form of aquatic locomotion: F1 is quadrupedal paddling,

F2 is alternate pelvic paddling, F3 is simultaneous pelvic paddling, F4 is dorsoventral pelvic undulation. Each B# refers to adaptations for an aquatic lifestyle: B1 is the reduction in relative length of cervical vertebrae, B2 is the caudalization of sacral vertebrae anteriorly-posteriorly, B3 is the disarticulation of the sacrum from the innominate, B4 is the increase in the length of the torso via lumbarization of the sacral, B5 is the increase in torso length by increasing the number of thoracolumbar vertebrae, B6 is the posterior movement of the maximal dorsoventral displacement during undulation, and B7 is the development of dorsoventrally compressed posterior caudal fluke vertebrae. B4 and B5 can be differentiated in that one can clearly see the change from sacral to lumbar vertebrae, where B5 is the addition of new thoracolumbar vertebrae. In addition, *Basilotritus* has been most recently been recognized as a synonym of *Pachycetus* (Uhen, 2014).

Anatomy and Function of the Appendicular Skeleton

While the axial skeleton usually provides the propulsive force for locomotion, in terrestrial artiodactyls and basal archaeocetes the appendicular skeleton provides surfaces for energy to be dispersed into water. The innominate consists of three fused bones: the ischium, ilium, and pubis (Evans et al., 2020). There is a left and right innominate, each mirroring the other across the sacrum. The pelvis is equated to the innominate, while the pelvic girdle also includes the sacrum (the fused sacral vertebrae). The ilium is the biggest bone in the innominate, characterized by its wing-like shape. The ischium is the bone in the innominate that helps to form the acetabulum, the hip socket in which the femoral head articulates. The pubis is a dorsoventrally compressed, curved bar of bone that is fused to the ilium and ischium (Evans et al., 2020). In terrestrial artiodactyls, the

innominate and sacrum are fused, however in many of the more derived archaeocetes lack articulation between the sacrum and innominate (Uhen, 2014). For terrestrial mammals, the pelvic girdle has the main role of supporting the animal's body weight and allowing for locomotion. Basal archaeocetes retained robust pelvic girdles, as while pelvic and foot-powered locomotion is inefficient, it still allowed for locomotion on land (Fish, 1996). As archaeocetes transitioned from paddling, or limb-based locomotion, in the water to dorsoventral undulation, or column-based locomotion, the pelvic girdle became reduced (Fish, 2000).

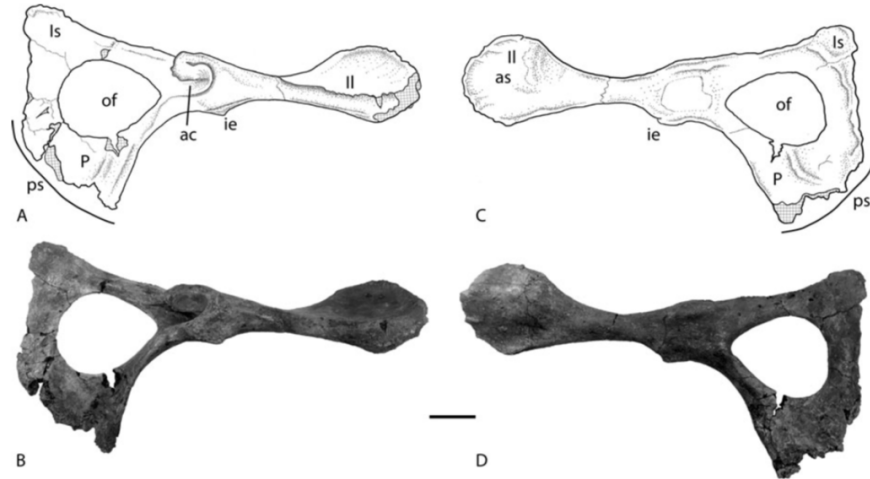


Figure 2 Right innominate of *Natchitochia jonesi* (MMNS VP-4849) in lateral (A, B) and medial (C, D) views. The scale bar is 10 cm. Areas of breakage are denoted by dashed regions. The labels represent: ac, acetabulum; as, auricular surface; cn, cotyloid notch; ie, iliopectineal eminence; Il, ilium; Is, ischium; of, obturator foramen; P, pubis; ps, pubic symphysis (Uhen, 2014).

Limbs are extremely important for the locomotion, social behaviors, and feeding of mammals (Polly, 2007). Part of the success of mammals over other taxa is likely due to their locomotor adaptability and wide range of locomotory habits (Kilbourne, 2021). The specialization in limb morphology, whether in terrestrial artiodactyls or cetaceans, is bound to the reduction of locomotor costs to suit their primary ecology (Kilbourne, 2021). In comparing the locomotion of terrestrial artiodactyls and archaeocetes, the hind limb is extremely valuable. The hind limb is composed of multiple long bones: the femur, tibia, and fibula (Evans et al., 2020). The femur is the largest long bone and supports the trunk along with the tibia and fibula. It articulates with the acetabulum in the innominate. The tibia is a long, thick bone that lies in the medial part of the hindlimb, articulating with the femur. The fibula is a long, thin laterally compressed bone that is positioned along the lateral part of the hind limb, also articulating with the femur (Evans et al., 2020). Together, these long bones support the weight of terrestrial artiodactyls and are utilized in hindlimb-powered aquatic locomotion for basal archaeocetes. Eventually, the long bones of the hindlimbs become completely vestigial for cetaceans, with only rudimentary remnants of the pelvic girdle left behind inside their body cavities (Tajima et al., 2004).

LOCOMOTOR MODES OF ARCHAEOCETES

Types of Locomotor Modes and Definitions

One of the most comprehensive and widely used models for cetacean locomotion was developed by Fish (1996) and revised Thewissen & Fish (1997) (Figure 1). The most basal and simplistic mode of aquatic locomotion is known as quadrupedal paddling. Quadrupedal paddling is the method by which mostly or fully terrestrial mammals swim, using alternating strokes of their four limbs. Quadrupedal paddling is essentially a modified terrestrial gait and shows no adaptation to aquatic environments. A common example of a quadrupedal paddler is the domestic dog. Pelvic paddling, the aquatic locomotor mode by which hindlimbs alone propel the body through water, is separated into two types: alternate pelvic paddling and simultaneous pelvic paddling. Alternate pelvic paddlers paddle one foot after the other on alternating beats, whereas simultaneous pelvic paddlers beat both hindlimbs at the same time. Undulation is an efficient, lift-based locomotor mode, in which sinusoidal waves run throughout the swimmer's body. Pelvic undulation, a locomotor mode uncommonly displayed in cetaceans, generates thrust via the sinusoidal movement of lumbar muscles. Caudal undulation is similar to pelvic undulation, however the propeller is the tail with force provided by the flexion and extension of both the lumbar and caudal vertebrae. Neither form of undulation is more derived, with each being differing paths of locomotion. Caudal oscillation utilizes

dorsoventral oscillations of the tail fluke to propel themselves through the water, with muscles of the back and abdomen providing a source of power (Thewissen and Fish, 1997). It is by this method that obligately aquatic cetaceans locomote, with posteriorly oriented flukes that oscillate in order to create thrust, whereas their anteriorly positioned flippers act as hydrofoils to maneuver and create lift to maintain stability in the water column (Segre et al., 2016).

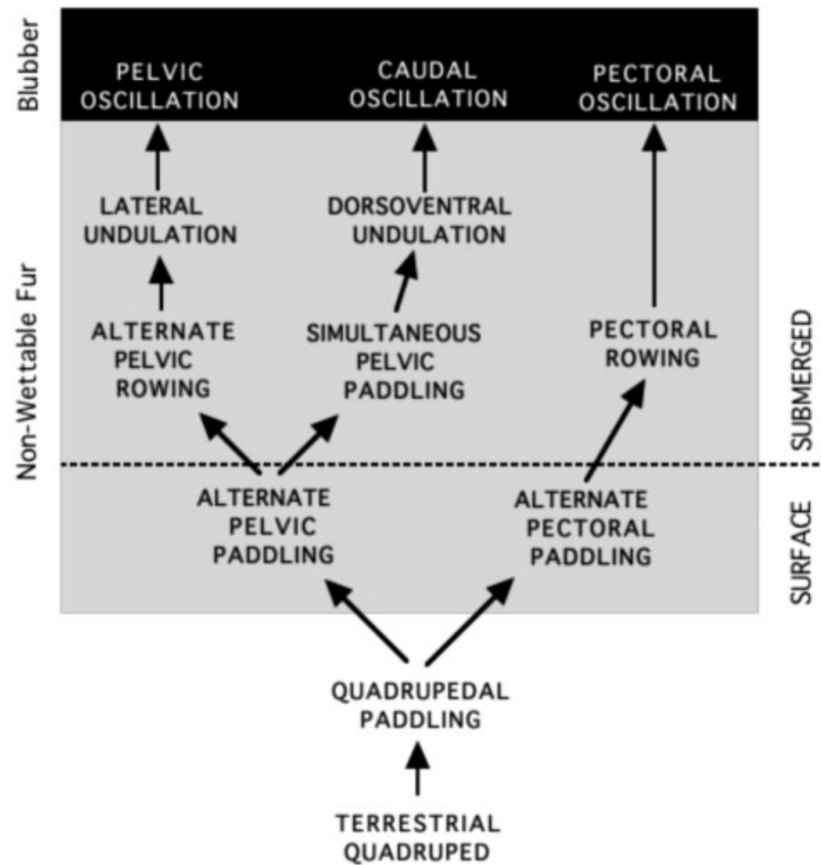


Figure 3. Model for mammalian aquatic locomotor stages and transitions, including a shift from surface to submerged locomotor modes and secondary aquatic adaptations (non-wettable fur, blubber) (Fish, 2016).

Aquatic Locomotion of Archaeocete Taxa

Locomotion in Pakicetidae

Pakicetus is a basal archaeocete from the early-middle Eocene of Pakistan that retains primitive characteristics, such as an underdeveloped auditory region (Gingerich and Russell, 1981). While pakicetids bear many terrestrial characters, such as cursorial

ankle and elbow adaptations, microstructural specializations indicate a more derived aquatic lifestyle (Madar, 2007). Pakicetids have hyperostosis and osteosclerosis throughout their postcranial skeleton, which are definitive aquatic characters. The increased weight of their skeletons would act as a ballast and aid in aquatic locomotion in shallow riverine and lacustrine environments, but it would have made a cursorial lifestyle too energy inefficient (Madar, 2007). Pakicetid innominata are large, with longer ischia than ilia, and their tibiae are long, though their tibial crests are significantly shorter (Thewissen et al., 2001b). While their long limb bones suggest cursory, the pachyosteosclerotic postcrania of pakicetids would have likely made running energetically inefficient. The expanded and elongated ischia of pakicetids would have provided points of attachment for hindlimb musculature, which would have aided in both terrestrial and aquatic locomotion (Bebej et al., 2016). *Pakicetus* likely utilized a form of quadrupedal paddling, though it may have helped stabilize its body with the tail while swimming (Gingerich et al., 2019).

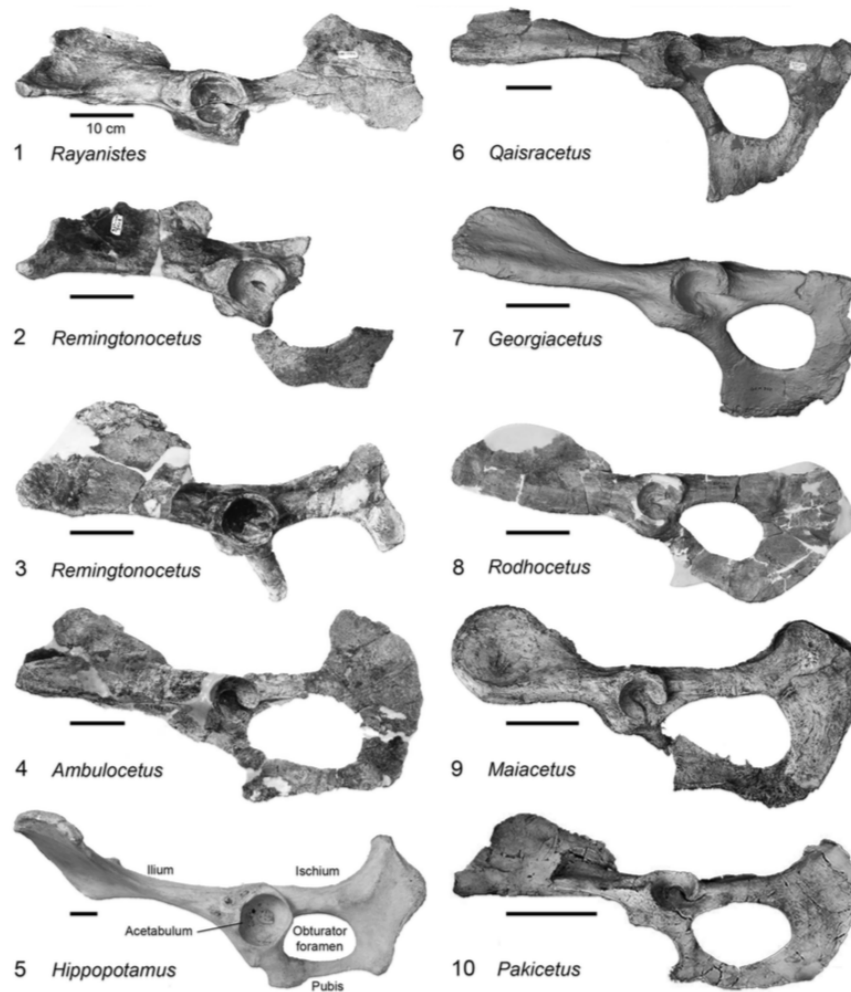


Figure 4 Left innominate of middle Eocene archaeocetes and a hippopotamus from Bebej et al. (2016), viewed laterally, with the anterior at the left. Most important skeletal anatomy is labeled on the hippopotamus innominate.

Locomotion in Ambulocetidae

Ambulocetidae is a family of basal archaeocetes that originated in the early middle Eocene of Indo-Pakistan (Uhen, 2010). *Ambulocetus natans* has adaptations for both terrestrial and aquatic locomotion, with large hindlimbs and feet, which suggests they had powerful musculature around the lumbus and innominate that would have helped propel them through the water (Gavazzi et al., 2020). There has been much debate on the locomotor mode of *Ambulocetus*, with Gavazzi et al (2020) claiming that it was likely a pelvic paddler and that it was unlikely that it used caudal undulation, since it has a dorsoventrally stable vertebral column. Many have compared the inferred aquatic locomotion of *Ambulocetus* to *Lutra* (otter), however Gingerich (2003) argues that lutrines trunk and limb proportions are still quite distinct from early archaeocetes, and so they aren't the best analogues. It is commonly favored, however, that due to the robust hindlimbs and feet and the dorsolateral expansion of the ischium that *Ambulocetus* was a powerful, foot-propelled swimmer. *Ambulocetus* probably generated thrust with the dorsoventral undulations of the lumbocaudal region, while utilizing the hindlimbs as hydrofoils (Madar et al., 2002).

Locomotion in Remingtonocetidae

Remingtonocetidae was a unique and derived family of archaeocetes from the early middle Eocene of Indo-Pakistan (Uhen, 2010). *Remingtonocetus domandaensis* maintained several terrestrial adaptations, such as a long neck held above the body, a fused four-vertebrae sacrum, and robust hindlimbs. Still, *Remingtonocetus* was probably somewhat limited on land because of a shallow fovea capitis on the femur, which would

reduce weight-bearing capabilities (Bebej et al., 2012). Morphological data from vertebrae, pelves, and femora indicate that *R. domandaensis* mostly swam using its hind limbs in pelvic paddling, and so it was not a specialized dorsoventral undulator. *R. domandaensis* was probably capable of flexing the lumbar region to increase pelvic paddling efficiency, the lumbus was not very mobile and so could not create thrust during aquatic locomotion (Bebej et al., 2012). Based on the vertebral column, *Kutchicetus minimus* swam utilizing a transitional locomotory mode, similar to *Ambulocetus natans* (Bajpai and Thewissen, 2000). While similar to *Remingtonocetus*, the robust hind limb, expansive innominate, and increased flexibility of the lumbar region suggest that *Rayanistes afer* was a more powerful, efficient, and maneuverable foot-powered swimmer (Bebej et al., 2016).

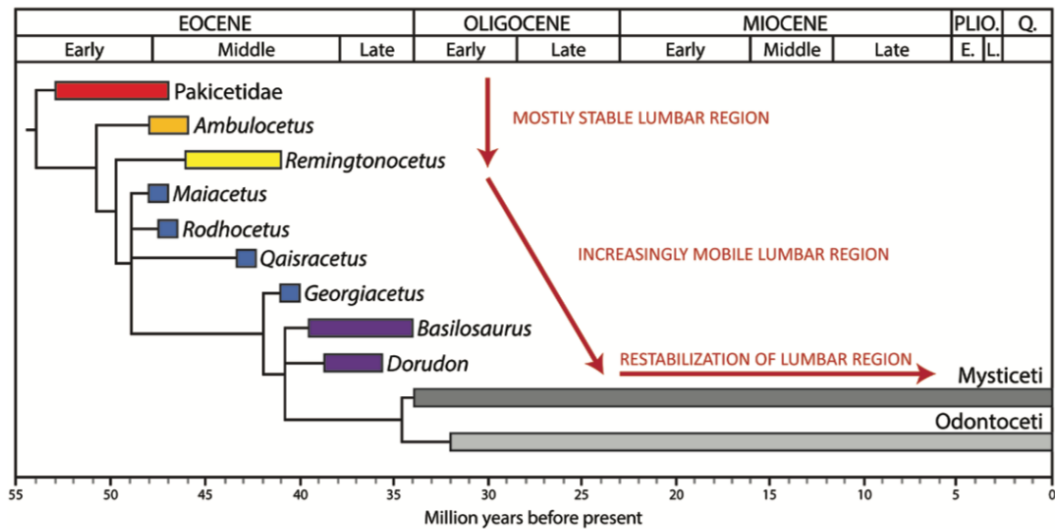


Figure 5 Cetaceans through time, including their phylogenetic relationships and mobility of their lumbar region from Bebej & Smith (2018).

Locomotion in Protocetidae

One of the largest and most widespread families of archaeocetes, Protocetidae originated during the early middle Eocene in Indo-Pakistan, however they quickly dispersed throughout the world's ocean basins to North Africa, Europe, North America, and western South America (Uhen, 2010). Protocetids were extremely diverse, with the most basal members retaining four, fused sacral vertebrae articulated to the innominate, while the most derived members lost their sacral vertebrae, which unarticulated with the innominate and became absorbed into the lumbocaudal vertebrae (Gavazzi et al., 2020).

The majority of protocetids propelled themselves through the water by utilizing their feet, with their hindlimbs attached to their vertebral column via a fused sacrum (Gingerich et al., 2019). *Rodhocetus kasrani* was a typical early protocetid with a precaudal vertebrae count similar to terrestrial mammals (Buchholtz, 2007). *Rodhocetus* likely swam using either pelvic paddling or caudal oscillation, or a combination of both (Uhen, 2014). *Maiacetus inuus* was similar to *Rodhocetus*, however it was considerably more adapted to an aquatic lifestyle, as it had more lumbar-dominated locomotion compared to purely hindlimb-powered locomotion (Gingerich et al., 2019). In addition, *Maiacetus* had feet that weren't as long as those of *Rodhocetus*, which suggest that it was not as specialized of a hindlimb-powered swimmer (Gingerich et al., 2009). *Peregocetus pacificus* shares similarities with *Maiacetus* and *Rodhocetus*, as it is a clear foot-powered swimmer (Lambert et al., 2019). *Peregocetus* was either an alternate or simultaneous pelvic hindlimb paddler, though it may have alternated between pelvic undulations of the hindlimbs and tail (Lambert et al., 2019). *Georgiacetus vogtlensis* is one of the most derived members of protocetidae, with elongated lumbocaudal vertebral centra and no iliosacral articulation. *Georgiacetus* would have been unable to support its own weight on land, and it would have moved in a similar manner to phocids (Hulbert et al., 1998). In other words, it would have used dorsoventral undulation to move on land, with their chest and pelvis making contact with the ground below (Kuhn and Frey, 2012). *Georgiacetus* probably swam via caudal undulation aided by lumbocaudal musculature, although it would have received secondarily significant assistance from the hindlimb (Hulbert et al., 1998). *Natchitochia jonesi* is very similar to *Georgiacetus*, except it still retains

articulation between the sacral vertebra and the innominate. *Natchitochia*, like *Georgiacetus*, probably swam via dorsoventral undulation to move their hindlimbs in water, though they wouldn't be able to caudally oscillate since they had no evidence of flukes (Uhen, 2014).

Locomotion in Basilosauridae

Basilosauridae is a cosmopolitan family of obligately aquatic archaeocetes that ranged from the late middle Eocene to the late Oligocene (Uhen, 2010). Basilosaurids had the most mobile lumbar region of any archaeocete family, and they were thought to have dorsoventrally undulated mostly with their lumbar and caudal vertebrae (Bebej and Smith, 2018). The hindlimbs of *Basilosaurus isis*, while reduced and too small to aid in locomotion, were possibly used to aid in acting as guides during copulation. This idea is based on knowledge of modern neocetes, whose reproductive organs are anchored by their pelvis (Gingerich et al., 1990).

Stages in the Evolution of Cetacean Swimming

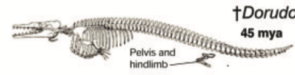
Osteology	Locomotor Mode	Performance Changes	Morphological Changes
	Terrestrial Quadruped		
	↓ †Pakicetids		
	Quadrupedal Paddling	• Move to water • Drag based propulsion	
	↓ †Ambulocetus		
	Alternate Pelvic Paddling	• Increased paddling efficiency • Buoyancy control	• Enlargement of hind feet • Interdigital webbing • Non-wettable fur
	↓ early †Protocetids		
	Simultaneous Pelvic Paddling	• Submerged swimming • Increased power and speed	• Elongate, dorsoventrally flattened tail
	↓ later †Protocetids		
	Undulation	• Reduced drag • Increased efficiency • Constant speed	• Reduction of hindlimbs • Expansion of tail at tip
	↓ modern whales		
	Caudal Oscillation	• Lift-based propulsion • Increased efficiency, power and speed • Elastic energy storage • Decreased pitching	• High aspect ratio flukes • Control of joint at peduncle • Loss of external hindlimbs

Figure 6 Summary of the changes to the aquatic locomotion, performance, and morphology across the evolution of Cetacea (Fish, 2016).

Aquatic Locomotion of Non-Archaeocete Taxa

Locomotion in Pinnipedia

Locomotion of Phocidae

Phocidae, known colloquially as “earless” or “true” seals, are the most well-adapted to marine life (Garrett and Fish, 2015). They are so well adapted to a marine ecology that they have given up many of their terrestrial adaptations in order to become

more efficient swimmers (Tennett et al., 2018). While the foreflippers can be used to help in pulling a phocid forward, mostly terrestrial locomotion consists of dorsoventral undulations of the spine (Tennett et al., 2018). Phocids generate thrust via horizontal undulations of their vertebral columns, which is assisted by extension and retraction of their hind flippers. Phocids thoracic region is very rigid, although their lumbar region is very flexible, and it provides enough flexibility for pelvic oscillations (Pierce et al., 2011). Cetaceans and phocids tend to undulate their bodies or make use of lateral and vertical oscillations of their bodies and hind appendages in a form of two-phase propulsive stroke pattern (Jeanniard-du-Dot et al., 2016). Phocids tend to move via lateral undulations of their caudal section of the body, which is done in sync with alternate medially positioned kicks of the hindlimbs, and the fore flippers tend to be pressed against the side of the body, being held still (Bryden, 1973). As the caudal part of the trunk moves laterally, from side to side, a fore flipper is extended and the whole limb is thrust with great force toward the medial part of the body. Some modern cetaceans may use a similar method to steer themselves with their fore flippers. The muscles that are most important in their aquatic locomotion are those associated with the spinal column of the caudal region, hind limbs muscles, and those that are used to extend and move the digits (Bryden, 1973).

Locomotion of Otariidae

Otariids, also known as “eared” seals, locomote significantly different from phocids, both terrestrially and aquatically. On land, otariids can walk quadrupedally,

using all four of their limbs, unlike phocids, which must inch along using dorsoventral body movements (Jeanniard-du-Dot et al., 2016). Otariids produce thrust during aquatic locomotion by utilizing their foreflippers, which are enlarged to increase surface area, and only use their hindflippers as a rudder to help maneuver sharp turns (Pierce et al., 2011). Otariids entire vertebral column is relatively mobile thanks to the flexibility of the intervertebral joints, which allows for a high level of maneuverability, which allows for tight turns during swimming. Their anterior thoracic region is also highly muscular, which allows for them to be efficient pectoral oscillators (Pierce et al., 2011). Otariids, instead of using their hindlimbs as a generator of thrust, make use of their forelimbs to create propulsion in the water in a four-phase stroke pattern, without having to distort their vertebral column (Jeanniard-du-Dot et al., 2016).

Locomotion of Odobenidae

Odobenids, while once including a diversity of different taxa, now is only represented by the modern walrus, *Odobenus rosmarus* (Pierce et al., 2011). Odobenids find themselves intermediate between phocids and otariids in terms of their locomotion. Terrestrially, odobenids are most similar to otariids, as they are able to walk using both their forelimbs and hindlimbs, rather than relying on the inch-worm like movements phocids use to move (Garrett and Fish, 2015). Aquatically, odobenids use both pelvic oscillation and pectoral oscillation, though they mostly favor pelvic oscillation, except during slow speeds where they make more use of their foreflippers. Odobenids have vertebral columns that are similar to those of phocids, however they are overall

intermediate between phocids and otariids, though their swimming style mostly consists of pelvic oscillation, with some pectoral oscillation (Pierce et al., 2011).

Locomotion in Sirenia

Sirenians are the only obligately marine mammal group other than cetaceans (Díaz-Berenguer et al., 2019). Modern sirenians are well adapted to life in the water, with fusiform bodies, short necks, rounded foreflippers, and a tail fluke (Frankini et al., 2021). In addition, sirenians possess bones that are pachyosteosclerotic, which help maintain buoyancy while swimming and feeding. While the earliest sirenians were quadrupedal and terrestrial, there are still significant differences in locomotion between the extant sirenian groups. Trichechids, or manatees, employ dorsoventral undulation, and possess tail flukes that are large and flat. Using the fluke and spine in conjunction, they produce a sinusoidal wave through their bodies. The shape and size of their fluke, and poorly developed muscles, mean that most trichechids are not great at swimming. Dugongids, however, are much more active, effective swimmers. While they swim with dorsoventral movements of their bodies, their flukes are wing-like. This allows them to perform more oscillatory dorsoventral movements, allowing to swim much faster when compared to trichechids. In both dugongids and trichechids, however, the pectoral flippers are used to steer the body while swimming, or to help anchor themselves to the substrate when feeding on vegetation (Frankini et al., 2021).

More basal sirenians retained four limbs, such as *Pezosiren* (Domning, 2001) and *Protosiren* (Díaz-Berenguer et al., 2019). While ancient dugongids (e.g. *Eotheroides*) already lost their hindlimbs and propelled themselves through the water via dorsoventral

undulation or oscillation, this wasn't the case for basal sirenians (Díaz-Berenguer et al., 2019). These basal, semiaquatic sirenians did not have tails powerful enough to propel themselves, likely having more otter-like tails, with some dorsoventral flattening, but lacking any kind of fluke (Domning, 2001). They would have been able to support themselves terrestrially, since their sacroiliac joint is strong, with the pelvis and sacrum still being fused. Basal sirenians likely propelled themselves in the water via extension of the spine, along with up and down movements of the hindlimbs at once. In other words, they would have most likely been simultaneous pelvic paddlers, with some dorsoventral undulation of the spine (Domning, 2001).

Locomotion in Mustelidae

Locomotion in Mustelinae

Most mustelids in the subfamily Mustelinae are terrestrial, with only a few taxa, such as *Neogale vision*, that inhabit aquatic ecosystems (Botton-Divet et al., 2018). Unlike lutrines, these mustelids are still mostly adapted to a terrestrial lifestyle, and so do not possess many of the traits characteristic of derived semi-aquatic mammals (Williams, 1983). As such, mustelids like *Neogale vision* locomote much like most terrestrial mammals do, with quadrupedal paddling. Alternate pelvic paddling can sometimes be observed, however quadrupedal paddling tends to dominate (Botton-Divet et al., 2018).

Locomotion in Lutrinae

Lutrines, such as *Enhydra lutris* and *Lontra canadensis*, are mustelids that are highly derived in their aquatic adaptations (Williams, 1989). While not as specialized as pinnipeds, many spend much of their lives in the water. Especially unusual is that many

lutrines are characterized by displaying multiple different modes of aquatic locomotion (Fish, 1994). *Lontra canadensis*, for instance, have been observed using quadrupedal paddling, forelimb paddling, hind-limb paddling, simultaneous hind-limb paddling, and dorsoventral undulation. Despite this variety in locomotor types, most lutrines predominantly use dorsoventral undulation or simultaneous pelvic paddling to swim. Interestingly, paddling modes of locomotion predominate while at the surface, but when submerged dorsoventral undulation takes over in its place (Fish, 1994).

Biomechanical Constraints on Locomotion

In Martín-Serra et al (2014), they found that of the influences on the shape of hindlimb bones, locomotor behavior and patterns had the least important effects. They argued then that this implies swimming style cannot be predicted from limb anatomy. Body size and phylogeny were the primary factors that influenced the morphology of hindlimb bones, not locomotor behavior. They argued that this result reflected the biomechanical trade-off between maintaining energetic efficiency and withstanding resistance to stresses. This trade-off can constrain the evolution of the shape of the appendicular (and axial) skeleton, and so limit overall morphological variability. However, Martín-Serra et al. (2014) were testing terrestrial carnivorans. Would semi to fully aquatic cetaceans be subject to the same constraints? I argue that a fluid medium like water doesn't impose the same biomechanical restraints as a terrestrial environment, and so there is more freedom for ecological innovation and experimentation with aquatic locomotion. In addition, they were testing only limb bones. The shape of the pelvis may not be driven by the same factors as the limb bones. Further support for this argument can

be found from another paper (Martin-Serra et al., 2015), which discusses that while the shape of appendicular bones covaries with robustness, it also covaries with ecological specialization. (Martin-Serra et al., 2015) go on to note that the innominate does not covary with bone robustness, probably due to the different structure and function from other appendicular bones. Again, the same authors (Martín-Serra et al., 2018) suggest that the flexibility of the modular pattern of the pelvic girdles of carnivorans could have arisen due to function and ecological specialization. Through my research I hope to understand if a similar relationship between the form and function (in terms of locomotor style) of the innominate can be identified. It is possible that reduction may be a response to selection pressures, such as ecological specialization, however it could also be attributed to a random loss of structural coherence caused by lack of selection?

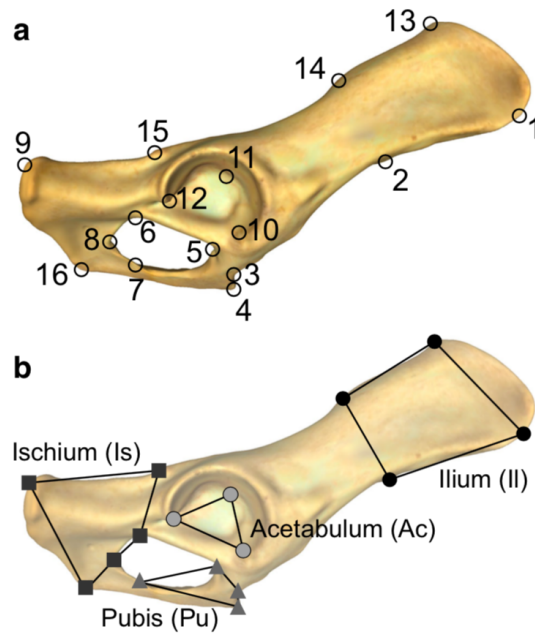


Figure 7 Three-dimensional landmarks and regions of the innominate of carnivorans. a, Locations of landmarks for geometric morphometric analyses. b, the four major developmental regions of the innominate (Martín-Serra et al., 2018).

GEOGRAPHY AND ENVIRONMENT OF EOCENE INDO-PAKISTAN

Plate Tectonics

The Paleocene-Eocene deposits of Indo-Pakistan make up a single tectonostratigraphic unit, being separated by Mesozoic marine shelf sediments below by a large unconformity and are separated above from the younger molasse via a

paraconformity from a period of non-deposition during the Latest Eocene and Early Oligocene (Wells, 1984). The Kohat Basin exists as part of an outcrop belt, with strata being exposed very steeply and upturned parallel to the Himalayas. Regression during the Early Eocene resulted in the formation of a saline, inland sea, which used to be open to the greater Tethys (Wells, 1984). India started travelling northwards, colliding with Tibet around the period between 50-55 Ma (Ali and Aitchison, 2008).

India likely first saw a biotic interchange with mainland Asia at about ~57 Ma, with the NE corner of India first colliding with Sumatra around ~35 Ma. It is during this period of collision when the fossil record indicates India-Asia faunal exchanges occurred (Ali and Aitchison, 2008).

Climate, Environment, and Ecology

The Paleocene-Eocene Thermal Maximum (PETM), a climatic event that saw a significant increase in global temperatures during the Paleocene-Eocene transition, is denoted by an abrupt warming of 5-10 °C. This shift is linked to the release of about 1050-2100 Gt of carbon via seafloor methane hydrate reservoirs (Bowen et al., 2004). Tanzanian stable isotopes suggest that sea surface temperatures were warmer than in modern seas on average (Pearson et al., 2007). Eocene climate models have been fairly consistent, showing that there were high concentrations of carbon dioxide (more than 10,000 pentagrams). During the transition from the end of the Eocene to the beginning of the Oligocene, there was a sharp shift from warmer temperatures to glacial conditions (Liu et al., 2009).

The Eocene fossil record of Indo-Pakistan is likely the result of multiple, filtered migrations between Asia, Europe, and Africa via travel over island arcs and straits (Thewissen and McKenna, 1992). The filtered migrations are also supported further by paleogeographical reconstructions of tectonics during the northward travel of Indo-Pakistan (Thewissen and McKenna, 1992). Evidence from fossil deposits in northern Indo-Pakistan suggest that in the Early to Middle Eocene, Asia was faunally distinct from Indo-Pakistan (Thewissen et al., 2001a). The most primitive archaeocetes have been found in shallow marine sedimentary rocks from the early to middle Eocene (Gingerich et al., 2001). These rock units were once part of the eastern Tethys Sea, which is now part of Indo-Pakistan (Gingerich et al., 2001). One of the most ancient and basal known cetaceans is *Pakicetus inachus*, described from the Early Eocene fluvial red sediments of the lower Kuldana Formation at Chorlakkhi in the Kohat District of Pakistan (Gingerich et al., 1983). Other species of *Pakicetus* are also known from the Kuldana Formation, though from different localities. While archaeocetes from the Middle Eocene are widespread, with taxa found in marine sediments from Egypt, Nigeria, and Texas, the oldest are from Indo-Pakistan. The fauna within the Kuldana Formation at Chorlakkhi associated with *Pakicetus inachus* are terrestrial mammals, gastropods, fishes, turtles, and crocodilians. All of the faunal remains are found close together in 10-40 cm beds of coarse calcareous granule stone within a 50 meter red shale sequence. The calcareous granules are most likely reworked soil nodules, which is interpreted based on their fabric of irregular concentric growth, formation of rings of hematite stains, and fractures similar to those of septarian nodules. Based on the stable isotopes of the carbonaceous granules

the environment appears to be terrestrial, and more specifically fluvial. This suggests fluvial environments were one of the places where the earliest archaeocetes began to explore and transition into living in the liquid medium. When Indo-Pakistan began to collide with Eurasia, it resulted in the trapping of microplates between the two landmasses. The result was that at the start of the Eocene, the Pakistan side of the eastern Tethys was confined by multiple consecutive shallow, linear basins that lay in between Indo-Pakistan and mainland Asia. Another outcome of Early Eocene tectonics was the Kohat depositional basin becoming enclosed, leaving it as a salty, epicontinental remnant sea. This epicontinental sea was very restricted in its circulation, evidence of which is provided by dolomite, gypsum, and halite deposits that are representative of marginal coastal environments. The transition from the coastal evaporites into the Kuldana continental red beds, and then back to more marine coastal evaporites suggests progradation of the basin-margin alluvial plains back into the basin during the formation of a shallow sea. There are many saline lakes and embayments that intrude interbed the lower Kuldana Formation, and all of which are high in primary plankton productivity and have an abundance of fish fossils. The Kohat Basin's shallow epicontinental sea of the Early Eocene, with its abundance in nutrients and food, would have been the perfect place for early archaeocetes to first transition into a marine lifestyle. The invasion of archaeocetes into the water was likely made possible by an increase in the intensity of oceanic upwelling, bringing with it plentiful nutrients that would have increased overall biotic productivity. It is also likely, however, that the first transition of whales into the sea occurred first in the shallow epicontinental remnants of the Tethys, and then they

moved into more offshore areas with intense upwelling. The length of the shoreline of the epicontinental sea would have been very extensive to the microplates that shifted along the western edge of Indo-Pakistan. It would be unlikely that the earliest cetaceans colonized regions of offshore sea without first living and adapting to nearshore, shallow areas (Gingerich et al., 1983).

The earliest whale is *Himalayacetus* (a genus of pakicetid), with the oldest remains being about 52.5 Ma from the Ypresian Subathu Formation of Kuthar Nala, India (Uhen, 2010). The oldest cetaceans come from Indo-Pakistan, which once was part of the Eocene Tethys Sea, a body of water which stood between mainland Asia and India during the beginning of their collision. Most of the earliest cetaceans in Indo-Pakistan date to the Ypresian, during the Late Early Eocene. The deposits from which Ypresian and Lutetian whales have been found in are variable, with *Pakicetus* being first described from fluvial red beds of the Kuldana Formation. With *Pakicetus* being initially described as the oldest cetacean, its presence in continental, fluvial deposits suggested that cetaceans first evolved in a freshwater habitat, before exploiting nearshore marine habitats. When *Himalayacetus* was discovered, however, it shifted the story, with it being an older specimen than *Pakicetus*, and found in the marine Subathu Formation. Equally old specimens are also found as part of backswamp deposits in the Panandhro lignite, and are freshwater in origin. Despite *Himalayacetus* being found in a marine deposit, both it and *Pakicetus* have oxygen isotopes in their tooth enamel that indicate they were mostly inhabiting freshwater. This may suggest that the earliest whales first explored continental, freshwater environments, such as rivers and lakes, before venturing into coastal, shallow

water environments. It did not take long for this transition from fresh to saltwater to occur, however, as late Lutetian *Babiacetus*, *Dalanistes*, and *Remingtonocetus* all have dental isotopes suggesting they lived in similar habitats to modern pinnipeds (Uhen, 2010).

MATERIALS & METHODS

Specimens

Archaeocetes: *Aegicetus gehennae* (CGM 60584), *Ambulocetus natans* (HGSP 18507), *Dalanistes ahmedi* (GSP-UM 3106), *Georgiacetus vogtlensis* (cast of GSM 350), *Maiacetus inuus* (GSP-UM 3551), *Pakicetus sp.* (HGSP 30313), *Qaisracetus arifi* (GSP-UM 3410), *Remingtonocetus domandaensis* (GSP-UM 3408), *Rodhocetus kasranii* (GSP-UM 3012), and *Ryanistes after* (CGM 42190).

Pinnipeds: *Cystophora cristata* (UMMZ 176889), *Odobenus rosmarus* (UMMZ 100780), *Pagophilus groenlandicus* (UMMZ 177446), *Phoca vitulina* (UMMZ 178152), *Pusa hispida* (UMMZ 101104), and *Zalophus californianus* (UMMP-R 1715).

Sirenians: *Eotheroides clavigerum* (UM 101219), *Eotheroides sandersi* (UM 97514), and *Protosiren smithae* (UM 94810).

Mustelids: *Enhydra lutris nereis* (UMMZ 156623), *Lontra canadensis canadensis* (UMMZ 100788), *Mustela putorius* (UMMZ 102705), and *Neogale vision energumenos* (UMMZ 98002).

Data collection

Landmark data was collected from the specimens listed above (except for *P. sp.* and *A. natans*, which already had landmark data collected by Dr. Uhen and Dr. Bebej) at the University of Michigan's Collections of Paleontology and Zoology across the second week of January, 2022. Three-dimensional landmark data was collected and digitized

on innominata using a Microscribe G2X. The microscribe is a mounted lever arm with an attached stylus, which in combination with a trigger activated handheld controller, allows landmark data to be captured to a high level of precision. Landmark data was directly recorded into Microsoft Excel.

Statistics

The landmark data, which were selected to best represent the three-dimensional shape of the innominata, transferred to the statistical software PAST to convert the coordinates into Procrustes coordinates. This process, known as a Procrustes fit, eliminated any effects of scaling, rotation, and translation. These Procrustes coordinates were then transferred back into excel to calculate the Procrustes distances, or the distances between two landmarks. These distances were chosen to include both the greatest number of taxa and greatest shape variation possible. Once the distances were calculated, they were again transported into PAST to calculate principal components analysis (PCA). A PCA is an exploratory technique which reveals along which hypothetical “components” carry the most variation. The loadings (which reveal what procrustes distances most influence variability in specific principal components) of this analysis allow one to interpret what is driving the variability visible in individual components.

3D Models

While at the University of Michigan, the specimens of *G. vogtlensis* and *D. ahmedi* were imaged and 3D models were created. The Paleontology Collections had a setup specifically for photogrammetry. This included a DSLR camera mounted on a

tripod, a photo blind, a turntable, small clear plastic cubes, and software (digicam, reality capture, and meshlab). The process began by balancing an innominate on a few clear plastic “ice cubes” on a white turntable. This was within the photo blind, which had walls of white cloth. This resulted in a completely white backdrop, allowing the imaging process to focus on the object. This also made clean up easier, since less background material was present. The imaging process then began, with the camera being placed at three angles: 90°, 60°, and 30°. This allowed most of the innominata to be imaged. The DSLR was connected to a PC, which had the software digicam open, which allowed for photos to be taken directly from the computer. The imaging process generally resulted in anywhere from 100-200 photos. These photos were then transferred to another PC, where they were all aligned using the photogrammetry software reality capture. Once a rough 3D model had been created, it was imported into meshlab to clean away any background material and give the model its final texture. Once this was done it could be uploaded to the UMORF website. In the time after my departure, models have also been created for multiple other archaeocete taxa, though the documentation for their upload is still ongoing, and so they are not yet available on UMORF.

RESULTS

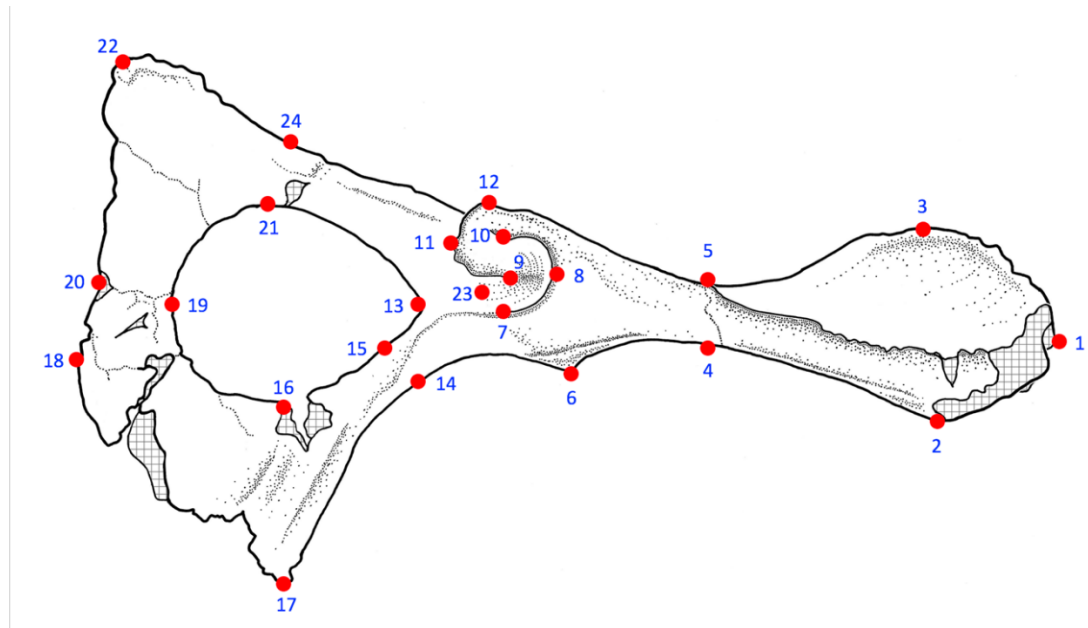


Figure 8 Sketch of archaeocete pelvis with collected landmarks. Landmarks number 1 to 24: 1. Anterior ilium 2. Ventralmost ilium 3. Dorsalmost ilium 4. Narrowest part of the ilial neck (no homology) 5. Narrowest part of the ilial neck (no homology) 6. Iliopectineal eminence 7. Ventral margin of semilunate surface 8. Anterior margin of semilunate surface 9. Anterior end of notch 10. Dorsal margin of semilunate surface 11. Posterodorsal margin of semilunate surface 12. Dorsal-posterior margin of acetabulum 13. Anteriormost margin of the obturator foramen 14. Narrowest ventral side of margin (no homology) 15. Narrowest dorsal side of margin (no homology) 16. Ventralmost margin of obturator foramen 17.

Anteroventralmost point of pubis 18. Posteriormost extent of pubic symphysis 19. Posteriormost extent of obturator foramen 20. Narrowest part of ischium posterior to obturator foramen 21. Dorsalmost extent of obturator foramen 22. Posterodorsalmost extent of the ischium 23. Posteroventral point of semilunate surface 24. Dorsal margin of ischium above obturator foramen.

Hypotheses

The terrestrial to aquatic transitional morphology of archaeocete postcrania helps characterize their aquatic locomotion. This thesis tests the hypothesis that the main driver of shape change of archaeocete innominata is the style of aquatic locomotion. A corollary of this hypothesis is that innominate shape is secondarily driven by phylogeny or possibly by osteological robustness. The null hypothesis is that aquatic locomotor style (as well as phylogeny and robustness) has no influence on the shape of archaeocete innominata.

Archaeocetes

For the first set of statistical analyses, only archaeocete taxa were compared with each other. In terms of landmark configuration, all principal component analyses were run with distances including landmarks 4, 5, 7, 8, 9, and 10. Distances measured were between landmarks 4 to 5, 4 to 7, 4 to 8, 5 to 7, 5 to 8, 5 to 10, 7 to 8, 7 to 9, 7 to 10, 8 to 9, 8 to 10, and 9 to 10. As can be seen in Figure 8, these landmark configurations represent distances between the narrowest part of the ilial neck to the narrowest part of the ilial neck (4 to 5), the narrowest part of the ilial neck to the ventral margin of the semilunate surface (4 to 7), the narrowest part of the ilial neck to the anterior margin of the semilunate surface (4 to 8), the narrowest part of the ilial neck to the ventral margin

of the semilunate surface (5 to 7), the narrowest part of the ilial neck to the anterior margin of the semilunate surface (5 to 8), the narrowest part of the ilial neck to the dorsal margin of the semilunate surface (5 to 10), the ventral margin of the semilunate surface to the anterior margin of the semilunate surface (7 to 8), the ventral margin of the semilunate surface to the anterior end of the notch (7 to 9), the ventral margin of the semilunate surface to the dorsal margin of the semilunate surface (7 to 10), the anterior margin of the semilunate surface to the anterior end of the notch (8 to 9), the anterior margin of the semilunate surface to the dorsal margin of the semilunate surface (8 to 10), and the anterior end of the notch to the dorsal margin of the semilunate surface (9 to 10). These distances were chosen based on the fragmentary remains of many fossil specimens (including archaeocetes and sirenians), since many specimens were so broken that only landmarks 4 through 10 could be recorded. The landmark configuration was chosen to both maximize as many critical taxa as possible, while also highlighting as much variation as possible. In this case, these distances highlight the ilium, which is what one would expect to be the most functionally important part of the innominate. This is because the ilium contains the acetabulum, which would have the strongest functional signal, since it articulates with the hind limb bones.

Table 1 Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete pelves.

PC	Eigenvalue	% variance
1	0.652148	73.216
2	0.130059	14.602
3	0.053041	5.955
4	0.0445766	5.005

As shown in table 1 and figure 15, most of the variance is within the first four main principal components. In particular, the first two components make up about 87% of variance, with components three and four being each about 5%. The scatter plot comparing components 1 and 2 (figure 9) appears to have 5 major groupings. Four taxa, *Rodhocetus kasranii*, *Dalanistes ahmedi*, *Maiacetus inuus*, and *Remingtonocetus domandaensis* occupy the lower right corner of the plot. *Pakicetus sp.* and *Ambulocetus natans* together occupy the upper left corner of the scatter plot. In the upper right corner of the plot, however, while *Ryanistes after* and *Qaisracetus arifi* are close in position, *Aegicetus gehennae* is alone in its occupation of the top left portion of the section. Lastly, *Georgiacetus vogtlensis* is the most isolated, being the only taxon in the lower left corner, being far towards the bottom left of the whole region.

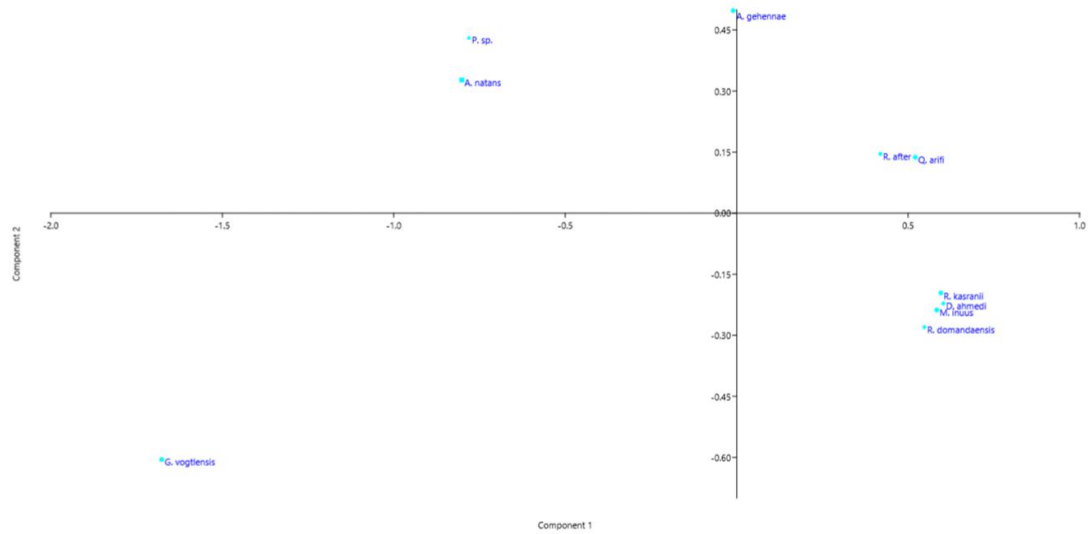


Figure 9 Scatter plot comparing the first and second principal components for distances measured on archaeocete pelvises. The light blue color represents archaeocetes, whereas the shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

When comparing components 1 and 3 (figure 10) the taxa are found within similar distances and positions on the plot. *R. after*, *Q. arifi*, *R. kasranii*, *D. ahmedi*, *M. inuus*, and *R. domandaensis* are all relatively close to each other, spread across the right side of the x-axis (component 3) in these upper and lower right corners. The other groupings are found in the same positions, though *A. gehennae* has been flipped from the

top to the bottom of the y-axis (component 1), while *G. vogtlensis* has moved slightly upwards from its corner position.

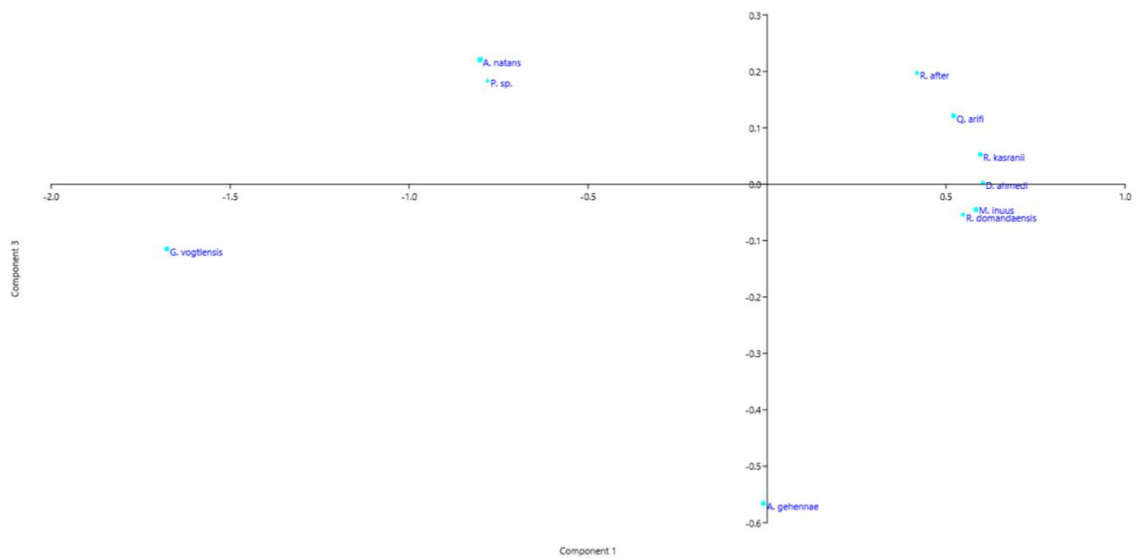


Figure 10 Scatter plot comparing the first and third principal components for distances measured on archaeocete pelvises. The light blue color represents archaeocetes, whereas the shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

While many of the same relationships are maintained when comparing components 1 and 4 (figure 11), the positions have changed dramatically for many. *P. sp.* and *A. natans* have moved from the top left corner to the bottom left corner, close to the

x-axis (component 4). The position of *G. vogtlensis* is most similar to its position when comparing components 3 and 4, however it has been flipped across component 4 to the upper right corner. *A. gehennae* has found itself towards the middle of the plot, though still far from most other taxa. The numerous taxa that once were held tightly together on the right side of the plot have now spread out. *Q. arifi* and *R. kasranii* have moved towards the top of the top right corner, whereas *R. domandaensis* and *M. inuus* have done the opposite, moving towards the bottom of the bottom right corner. *D. ahmedi* and *R. after* are relatively close, and are much closer to *R. domandaensis* and *M. inuus* than to *Q. arifi* and *R. kasranii*.

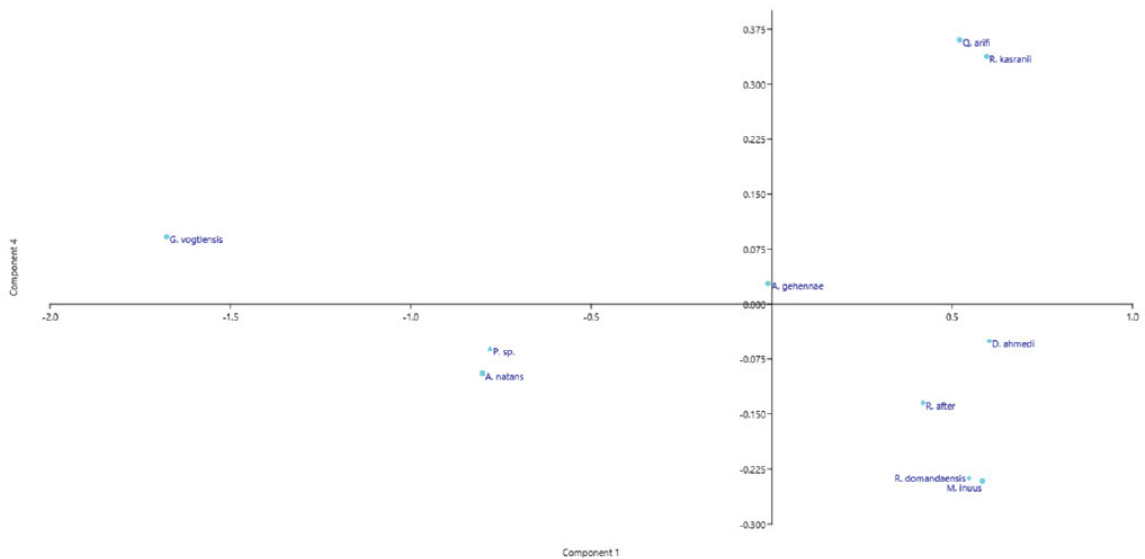


Figure 11 Scatter plot comparing the first and fourth principal components for distances measured on archaeocete pelves. The light blue color represents archaeocetes, whereas the shape of each point refers to

smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

When comparing components 2 and 3 (figure 12) one can still find the same relationships between taxa. *G. vogtlensis* is still isolated on its own, just as *A. gehennae* is. The other four pairs of taxa still seem to be found close together, with *A. natans* and *P. sp.* in the far top right corner of the map, not far from *R. after* and *Q. arifi*. *R. kasranii* and *D. ahmedi*, too, are close together, with *M. inuus* and *R. domandaensis* just below.

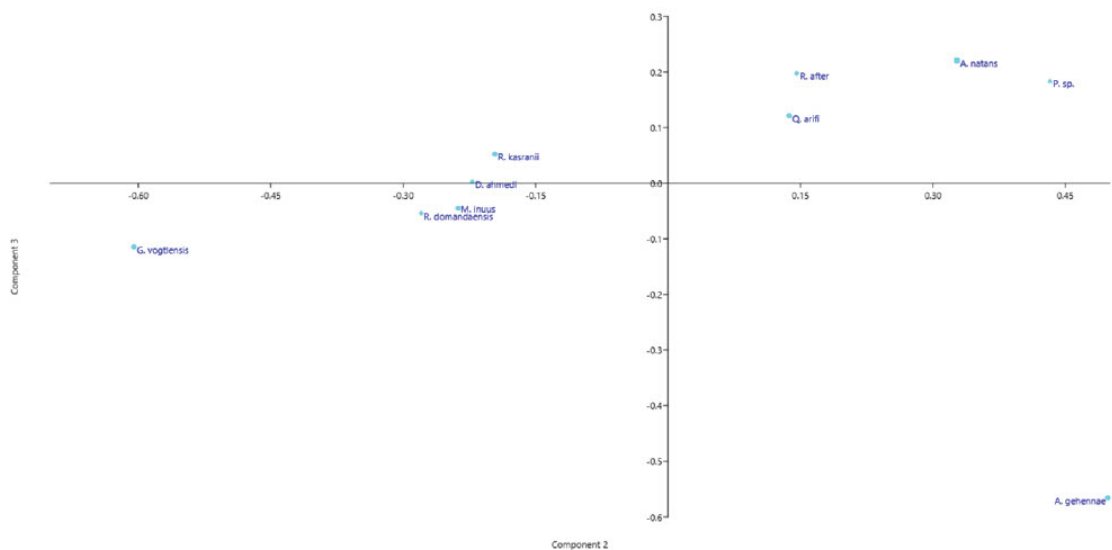


Figure 12 Scatter plot comparing the second and third principal components for distances measured on archaeocete pelves. The light blue color represents archaeocetes, whereas the shape of each point refers to

smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

The relationships displayed in previous plots are not as visible when comparing components 2 and 4 (figure 13). While taxa, such as *A. gehennae* and *G. vogtlensis*, are still isolated, the shared positions between *D. ahmedi* and *R. after* and *R. kasranii* and *Q. arifi* have been mostly lost, though they appear to be mirrored across component 2. *P. sp.* and *A. natans* and *R. domandaensis* and *M. inuus* still appear to share their approximate spatial relationships, however.

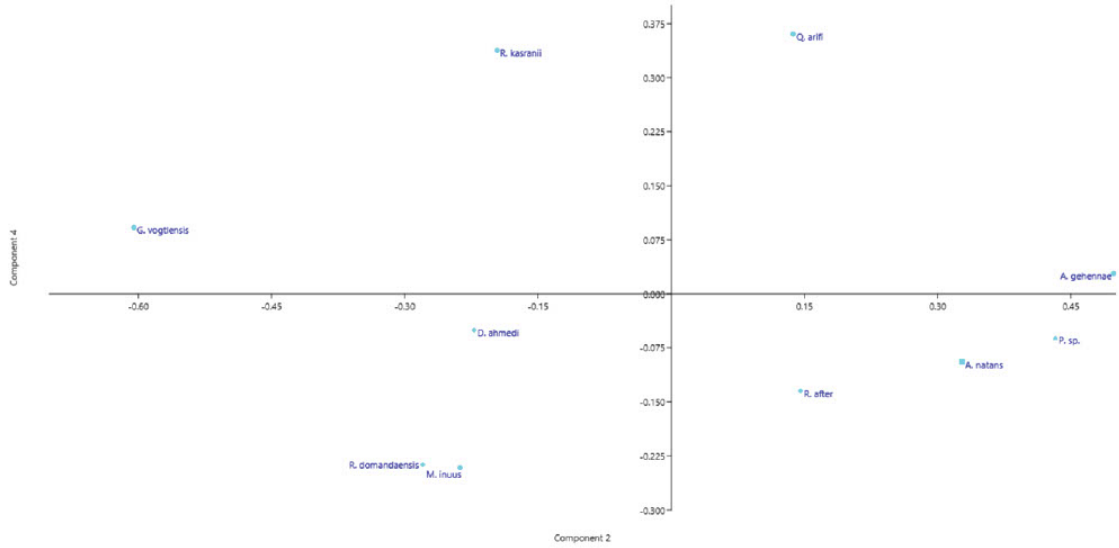


Figure 13 Scatter plot comparing the second and fourth principal components for distances measured on archaeocete pelvises. The light blue color represents archaeocetes, whereas the shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

The last plot (figure 14), which compares the third and fourth principal components, is only majorly different in the position of *R. after* and *G. vogtlensis*. While *R. after* is typically closest in position to *D. ahmedi*, in this case it is closer to *P. sp.* and *A. natans*. *G. vogtlensis*, while normally isolated, is fairly close to *D. ahmedi*, with both being close to the center of the plot.

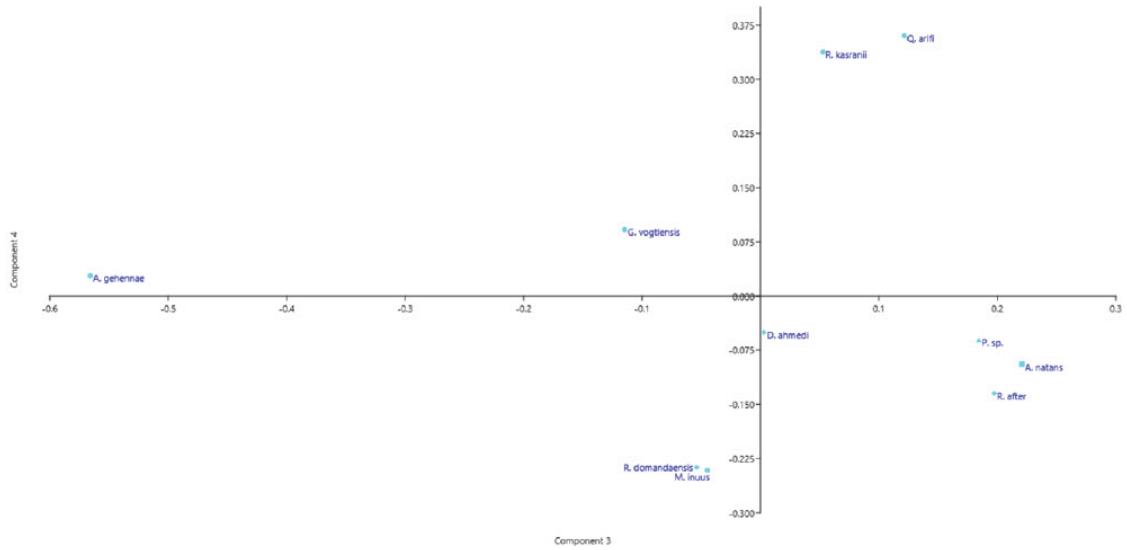


Figure 14 Scatter plot comparing the third and fourth principal components for distances measured on archaeocete pelvises. The light blue color represents archaeocetes, whereas the shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆).

In terms of loadings (table 2), the first principal component explains much of the positive variation for distances 4 to 5, 5 to 7, 5 to 8, and 5 to 10. The second principal component makes up most of the positive variation for distances 4 to 7, 7 to 8, and 7 to 10. It also makes up some of the positive variation for 4 to 8, 5 to 10, 7 to 9, 8 to 9, 8 to 10, and 9 to 10. The third principal component makes up most of the variation for distances 4 to 8, 5 to 7, and 7 to 9. It also makes up some of the positive variation for

distance 9 to 10. The third principal component makes up a lot of the negative variation for distances 4 to 5, 5 to 8, 7 to 8, and 8 to 10. The fourth principal component represents most of the positive variation for distances 7 to 9, 8 to 9, 8 to 10, and 9 to 10. The fourth principal component also makes up some of the positive variation for 7 to 10 and most of the negative variation for 4 to 7, 4 to 8, and 5 to 10. While there are more than four principal components (see figure 17), any component after the fourth makes up only fractions of a percent of the total variability, and so isn't worth examining further.

Table 2 Loadings for all principal components for distances measured on archaeocete pelves.

Procrustes Distances	Anatomical Distances	PC 1	PC 2	PC 3	PC 4
4 to 5	narrowest part of the ilial neck to the narrowest part of the ilial neck	0.52851	-0.062695	-0.35324	-0.075612
4 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	-0.094721	0.64034	-0.058986	-0.30496
4 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	-0.049318	0.32565	0.46978	-0.25857
5 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	0.44085	0.018038	0.58909	-0.079798

5 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	0.50976	0.050773	-0.21661	- 0.0018244
5 to 10	narrowest part of the ilial neck to the dorsal margin of the semilunate surface	0.46898	0.13249	0.025832	-0.2364
7 to 8	ventral margin of the semilunate surface to the anterior margin of the semilunate surface	-0.052016	0.41396	-0.39987	-0.032228
7 to 9	ventral margin of the semilunate surface to the anterior end of the notch	0.098706	0.14955	0.21355	0.58317
7 to 10	ventral margin of the semilunate surface to the dorsal margin of the semilunate surface	-0.04416	0.43182	-0.041126	0.13145
8 to 9	anterior margin of the semilunate surface to the anterior end of the notch	0.094858	0.18745	-0.0065553	0.4818
8 to 10	anterior margin of the semilunate surface to the dorsal margin of the semilunate surface	0.087012	0.12895	-0.13363	0.33845
9 to 10	anterior end of the notch to the dorsal margin of the semilunate surface	0.064538	0.16606	0.17707	0.259

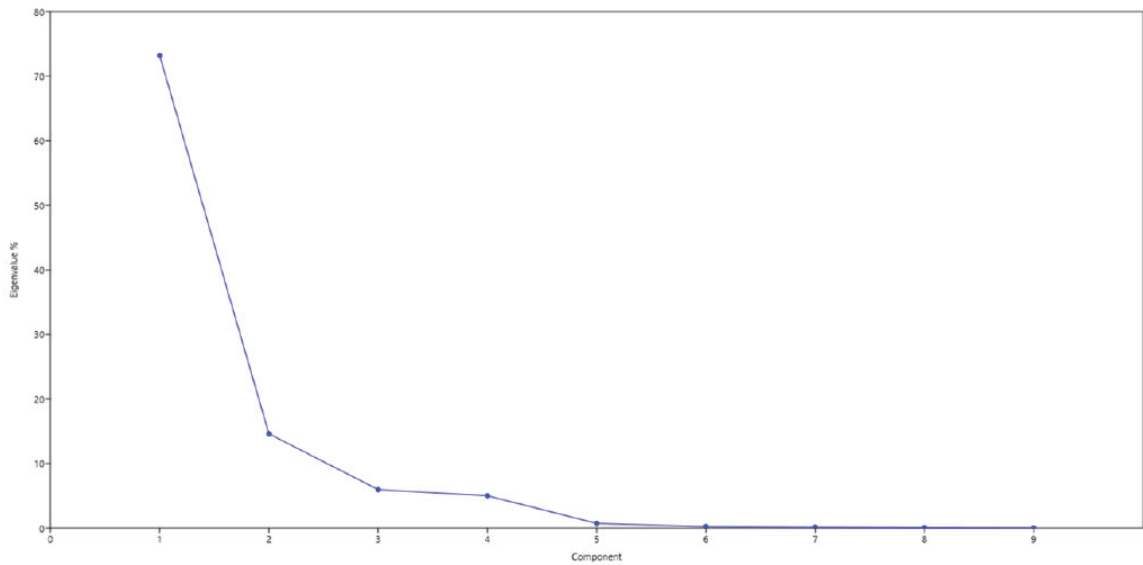


Figure 15 Scree plot showing how much variation is covered in each principal component for distances measured on archaeocete pelves.

Archaeocetes & Pinnipeds

Table 3 Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and pinniped pelves.

PC	Eigenvalue	% variance
1	0.483466	50.214
2	0.240328	24.961
3	0.102414	10.637
4	0.0614526	6.383

For the second set of statistical analyses, principal component analyses are run for archaeocetes and pinnipeds together. They use the same landmark configuration and same distances as the previous analysis of archaeocetes, so to be more easily comparable. As seen in table 3 and figure 22, most of the variability is within the first four main principal components. In particular, the first two components make up about 74% of variance, with components three and four making up the remaining 16%. The scatter plot comparing components 1 and 2 (figure 16) appears to have similar groupings to the original archaeocete principal components analysis, however the addition of pinnipeds has changed some aspects. *Phoca vitulina* and *Pagophilus groenlandicus* group close together, towards the top right of the upper left corner of the plot. They share this area with both *Qaisracetus arifi* and *Rodhocetus kasranii*. *Zalophus californianus* and *Pusa hispida* also group close together, though they are located in the midsection of the upper right corner of the plot. *Odobenus rosmarus* plots near the center of the graph, not far from *Aegicetus gehennae*. *Cystophora cristata* is isolated on its own, though it shares the upper left corner of the plot with *P. vitulina*, *P. groenlandicus*, and *O. rosmarus*. Overall, the archaeocetes and pinnipeds may be statistically separable based on how the group.

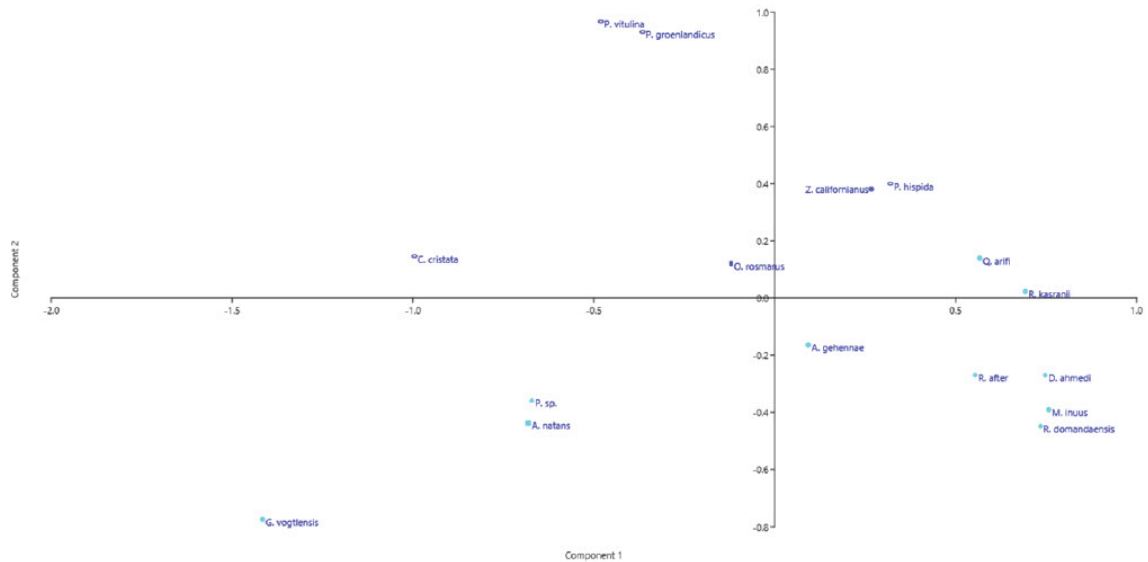


Figure 16 Scatter plot comparing the first and second principal components for distances measured on archaeocete and pinniped pelves. The light blue color represents archaeocetes and the dark blue color represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (⊗), and Odobenidae (▮).

When comparing the first and third principal components (figure 17) for archaeocetes and pinnipeds, most of the relationships are maintained, however there are some major changes. While with the first and second principal components *Z. californianus* and *P. hispida* were close in position, here *P. hispida* is close to a cluster which includes *R. domandaensis*, *D. ahmedi*, *M. inuus*, and *R. kasranii*. *Z. californianus*,

on the other hand, is close to *A. gehennae*, *R. after*, and *Q. arifi*. *P. vitulina* and *P. groenlandicus* are still close in position, as well as *O. rosmarus* and *A. gehennae*. Overall, many of the archaeocetes appear to cluster more closely than some of the pinnipeds. *G. vogtlensis* is still far removed, however, which may be due to its overall shape, which is more distinct when compared to other protocetids and archaeocetes in general.

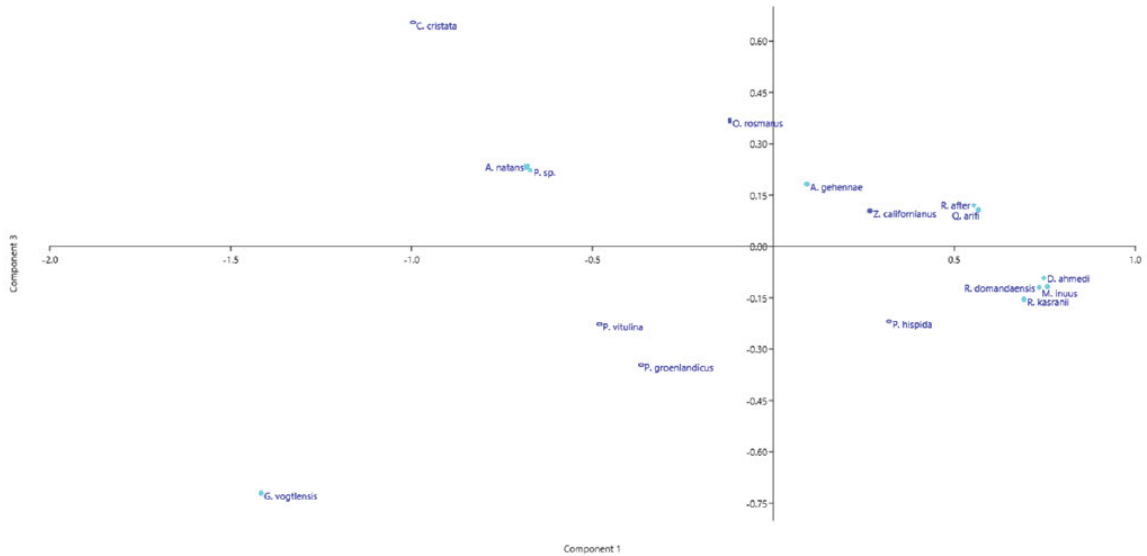


Figure 17 Scatter plot comparing the first and third principal components for distances measured on archaeocete and pinniped pelves. The light blue color represents archaeocetes and the dark blue color represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (⊗), and Odobenidae (▮).

The first and fourth principal components (figure 18) only see a few changes from the previous comparisons. *Z. californianus* and *P. hispida* are again close in position, though they also are close to the cluster of archaeocetes that include *R. domandaensis*, *R. kasranii*, *D. ahmedi*, *M. inuus*, and *Q. arifi*. *P. sp.* and *A. natans* are close to *P. vitulina* and *P. groenlandicus*, sharing the upper left portion of the scatter plot. *C. cristata* is relatively close in position to *G. vogtensis*, with both of them being isolated in the lower left corner of the plot. *O. rosmarus* stills keeps close to the center of the graph, not far from *P. groenlandicus*.

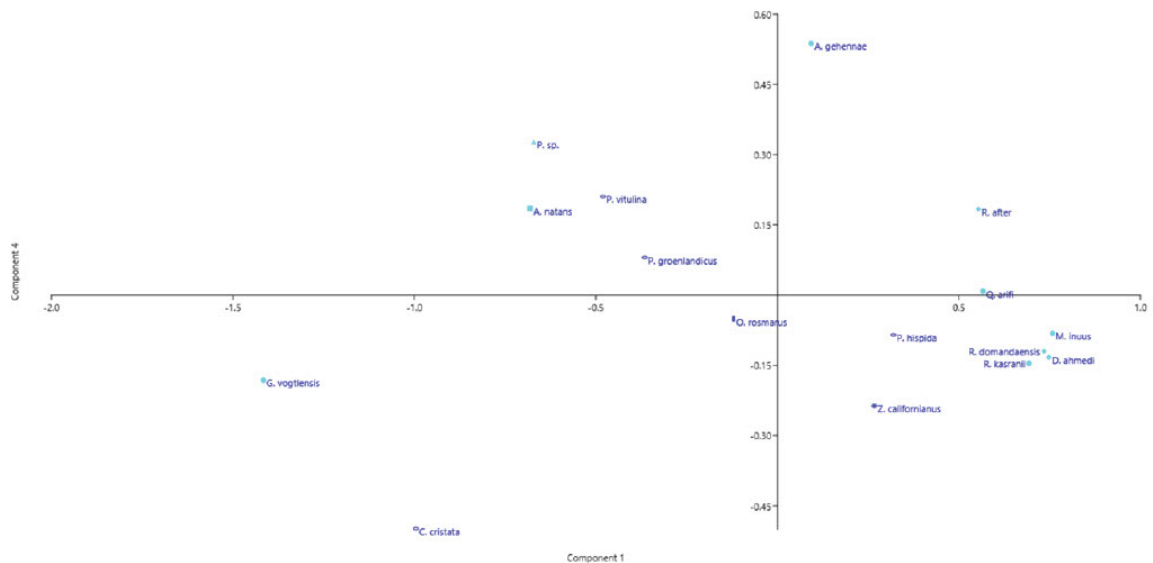


Figure 18 Scatter plot comparing the first and fourth principal components for distances measured on archaeocete and pinniped pelves. The light blue color represents archaeocetes and the dark blue color

represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), and Odobenidae (▮).

When comparing the second and third principal components (figure 19), one of the most apparent changes is to the cluster of protocetids and remingtonocetids, which has now spread out over a larger area. Despite this, *R. domandaensis* and *M. inuus* still plot close together, although *D. ahmedi*, *R. after*, *Q. arifi*, and *R. kasranii* are further away. *O. rosmarus* is midway between *Q. arifi* and *C. cristata*. *Z. californianus* remains relatively close to *P. hispida*, and is also nearby to *Q. arifi*. *P. vitulina* and *P. groenlandicus*, while in close proximity to each other, remain relatively isolated from the other taxa.

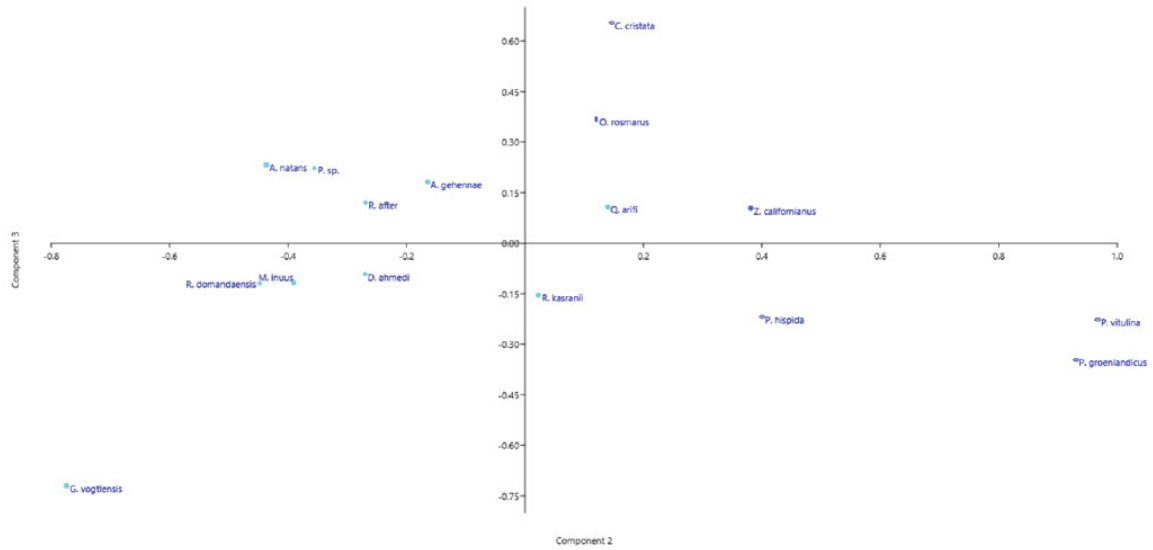


Figure 19 Scatter plot comparing the second and third principal components for distances measured on archaeocete and pinniped pelves. The light blue color represents archaeocetes and the dark blue color represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), and Odobenidae (▮).

The second and fourth components (figure 20) are very similar to the comparison between the second and third components, with almost all of the major spatial relationships appearing to remain. Many taxa, such as *P. vitulina* and *P. groenlandicus*, have simply been flipped across an axis (component 4). *C. cristata*, however, has become more isolated, with an increased distance from *O. rosmanus*. Meanwhile, *O. rosmanus* is

now held tightly close between *Q. arifi* and *R. kasranii*. As mentioned in the discussion of the first two components, it looks like there is a distinct separation of archaeocetes from pinnipeds.

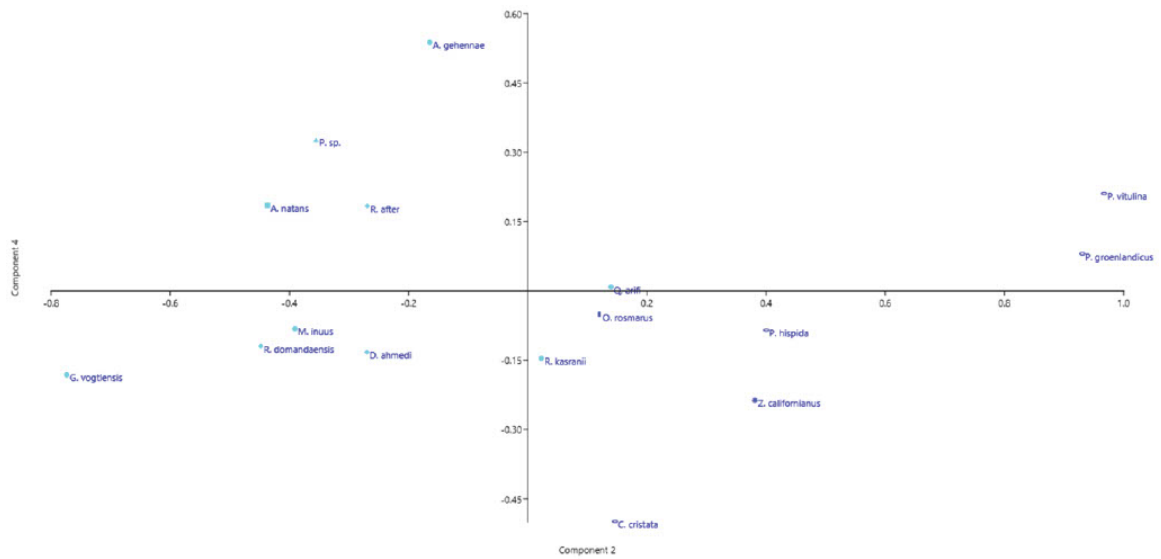


Figure 20 Scatter plot comparing the second and fourth principal components for distances measured on archaeocete and pinniped pelves. The light blue color represents archaeocetes and the dark blue color represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), and Odobenidae (▮).

In the final plot, comparing the third and fourth components (figure 21), *P. hispida* is very close in position to *M. inuus*, *R. domandensis*, and *R. kasranii*. *P. vitulina* and *P. groenlandicus* are still closely positioned, however they are close to the

aforementioned cluster, rather than being isolated as in the previous plot. *Z. californianus* and *O. rosmarus* are slightly distant from other taxa, occupying the lower right corner of the plot. Both *G. vogtlensis* and *A. gehennae* are isolated from other taxa, though are found in near opposite sides.

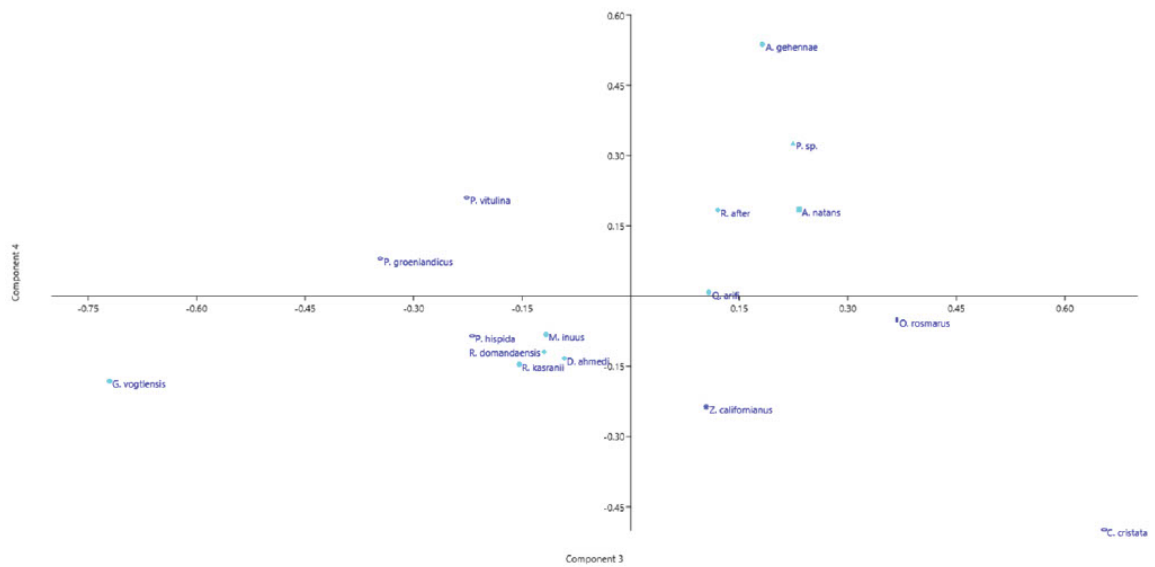


Figure 21 Scatter plot comparing the third and fourth principal components for distances measured on archaeocete and pinniped pelvises. The light blue color represents archaeocetes and the dark blue color represents pinnipeds. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Phocidae (○), Otariidae (⊗), and Odobenidae (▮).

In terms of loadings (table 4), the first principal component explains much of the positive variation for distances 4 to 5, 5 to 7, 5 to 8, and 5 to 10. It also explains some of negative variability for distances 4 to 8, 7 to 8, and 7 to 10. The second principal component makes up most of the positive variation for distances 7 to 9, 7 to 10, 8 to 9, and 8 to 10. It also makes up some of the positive variation for 4 to 5, 5 to 7, 5 to 8, and 9 to 10. In addition, the second component also makes up most of the negative variation for distance 5 to 10 and some of the negative variation for distance 4 to 7. The third principal component makes up most of the positive variation for distances 4 to 7, 4 to 8, and 7 to 8. It also makes up some of the positive variation for distance 4 to 5, 5 to 7, 5 to 10, 7 to 9, 7 to 10, and 9 to 10. The third principal component makes up a lot of the negative variation for distances 5 to 8 and 8 to 10. The fourth principal component represents most of the positive variation for distance 4 to 7. The fourth principal component also makes up some of the positive variation for 5 to 8, 5 to 10, 7 to 10, 8 to 9, 8 to 10, and 9 to 10 and most of the negative variation for distances 4 to 5, 5 to 7, and 7 to 9.

Table 4 Loadings for all principal components for distances measured on archaeocete and pinniped pelvises.

Procrustes Distances	Anatomical Distances	PC 1	PC 2	PC 3	PC 4
4 to 5	narrowest part of the ilial neck to the narrowest part of the ilial neck	0.46866	0.15436	0.1217	-0.24818
4 to 7	narrowest part of the ilial neck to the	-0.065831	-0.12337	0.34027	0.6802

	ventral margin of the semilunate surface				
4 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	-0.11548	0.0055507	0.42893	- 0.0019666
5 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	0.36474	0.19755	0.2496	-0.31482
5 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	0.52079	0.2051	-0.18006	-0.30319
5 to 10	narrowest part of the ilial neck to the dorsal margin of the semilunate surface	0.55431	-0.35827	-0.18006	0.30319
7 to 8	ventral margin of the semilunate surface to the anterior margin of the semilunate surface	-0.12154	-0.031174	0.53046	0.039059
7 to 9	ventral margin of the semilunate surface to the anterior end of the notch	5.385E-05	0.35601	0.21355	0.58317
7 to 10	ventral margin of the semilunate surface to the dorsal margin of the semilunate surface	-0.04416	0.43182	0.21427	0.1286
8 to 9	anterior margin of the semilunate surface to the anterior end of the notch	0.042499	0.3364	0.064211	0.1107

8 to 10	anterior margin of the semilunate surface to the dorsal margin of the semilunate surface	0.028303	0.46703	-0.32303	0.36109
9 to 10	anterior end of the notch to the dorsal margin of the semilunate surface	0.0099245	0.18526	0.10679	0.11227

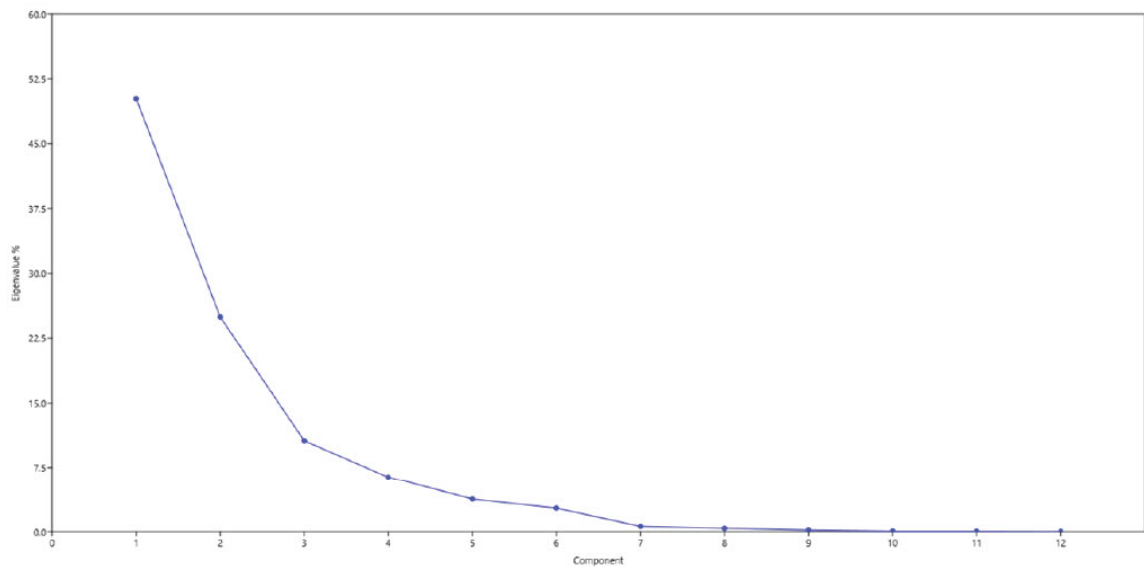


Figure 22 Scree plot showing how much variation is covered in each principal component for distances measured on archaeocete and pinniped pelves.

Archaeocetes & Sirenians

Table 5 Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelves.

PC	Eigenvalue	% variance
1	0.5058	68.454
2	0.119717	16.202
3	0.0574695	7.778
4	0.040083	5.425

For the third set of statistical analyses, principal component analyses are run for archaeocetes and sirenians together. They use the same landmark configuration and same distances as the previous analysis of archaeocetes and pinnipeds. As seen in table 5 and figure 29, most of the variability is within the first four main principal components. In particular, the first two components make up about 84% of variance, with components three and four making up the remaining 12%. The scatter plot comparing components 1 and 2 (figure 23) appears to have similar groupings to the original archaeocete and pinniped principal components analysis, however the addition of sirenians has changed some parts. The sirenians, *Eotheroides sandersi*, *Eotheroides clavigerum*, and *Protosiren smithae* all group closely together in the lower right portion of the scatter plot. *P. smithae* groups most closely with *E. sandersi*, though *E. clavigerum* is not far. The sirenians group close with a cluster of archaeocetes that includes *Dalanistes ahmedi*, *Maiacetus*

inuus, and *Remingtonocetus domandaensis*. The other groupings of archaeocetes remain relatively unchanged compared to analyses from earlier sets.

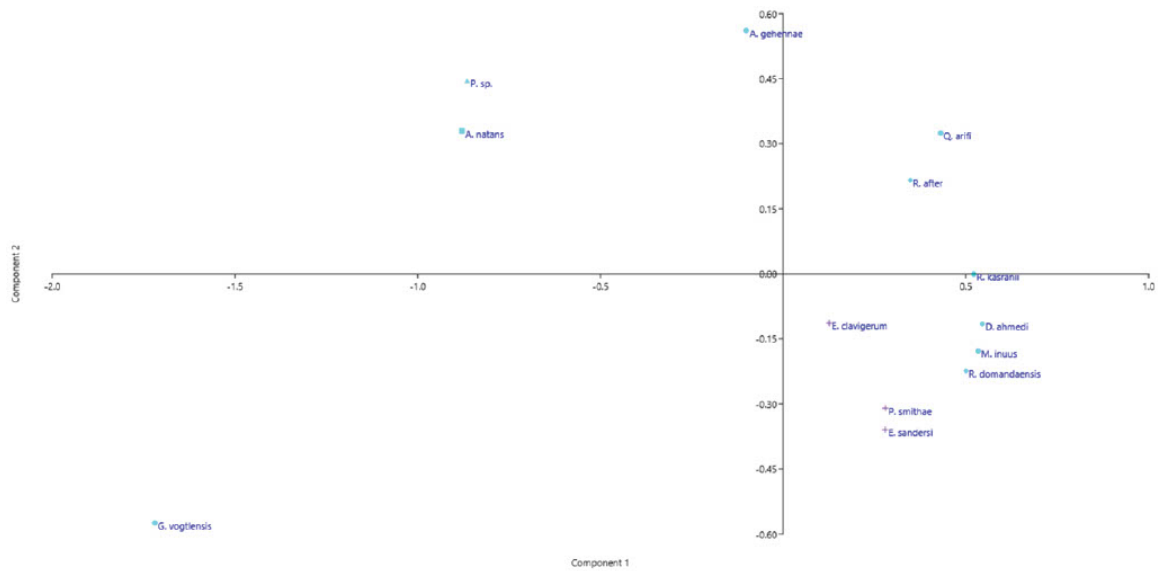


Figure 23 Scatter plot comparing the first and second principal components for distances measured on archaeocete and sirenian pelvises. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelvises. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups:

Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

When comparing the first and third principal components (figure 24), the sirenians, while still located in the bottom right corner of the plot, have spread out. While *P. smithae* and *E. clavigerum* have not moved very far, *E. sandersi* is almost over the x-axis

(component 3) towards *D. ahmedi*. *E. sandersi* remains closest to *R. after*, and is nearby to the clustered *R. domandaensis* and *M. inuus*. *G. vogtlensis* appears to retain its isolated position regardless of which group it is compared to.

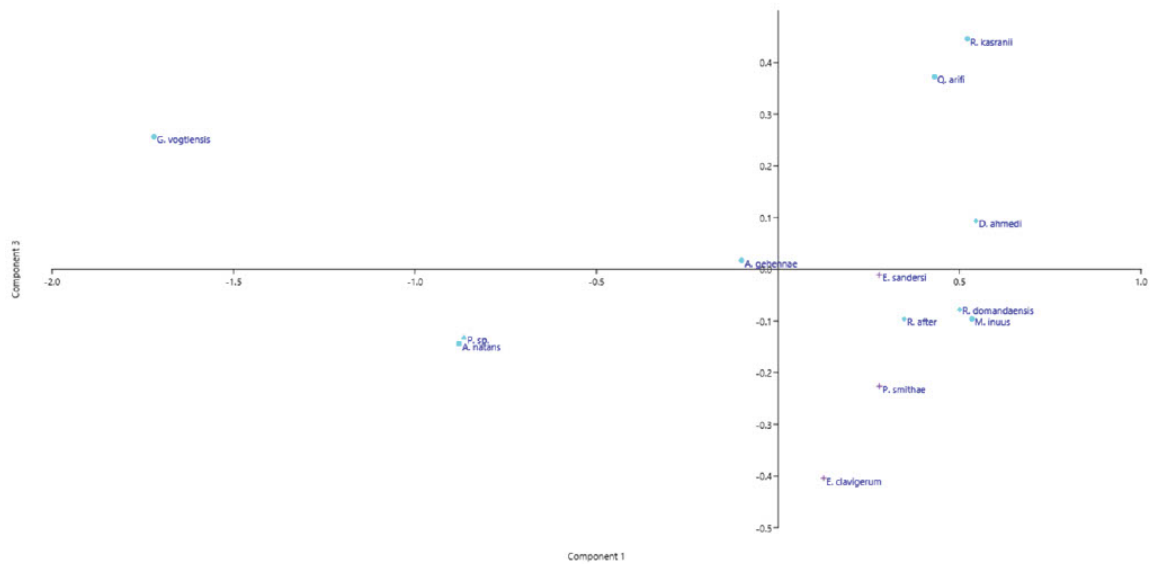


Figure 24 Scatter plot comparing the first and third principal components for distances measured on archaeocete and sirenian pelvises. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelvises. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

Looking at the first and fourth principal components together (figure 25), we see some major spatial shifts, though the relationships between sirenians have not changed

much. *E. clavigerum* has moved above the x-axis (component four) to the upper right corner of the plot, however the closely positioned *E. sandersi* and *P. smithae* lay just beneath it. *E. clavigerum* is closest to the two other sirenians, although none are far from the cluster of protocetids and remingtonocetids.

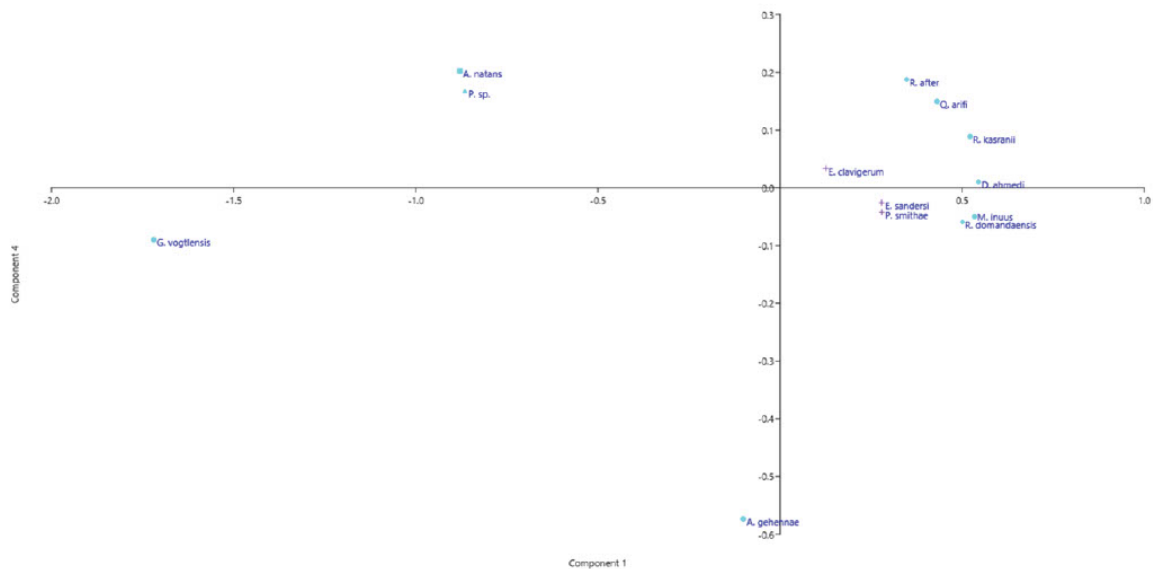


Figure 25 Scatter plot comparing the first and fourth principal components for distances measured on archaeocete and sirenian pelves. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelves. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

When comparing the second and third principal components (figure 26), the sirenians have again spread out, though still remain almost equidistant from each other. *E. clavigerum* is a bit further away, though each sirenian surrounds the closely positioned *R. domandaensis* and *M. inuus*. All other archaeocete taxa are much further from the sirenians, with the sirenians being more isolated in the bottom left corner of the plot.

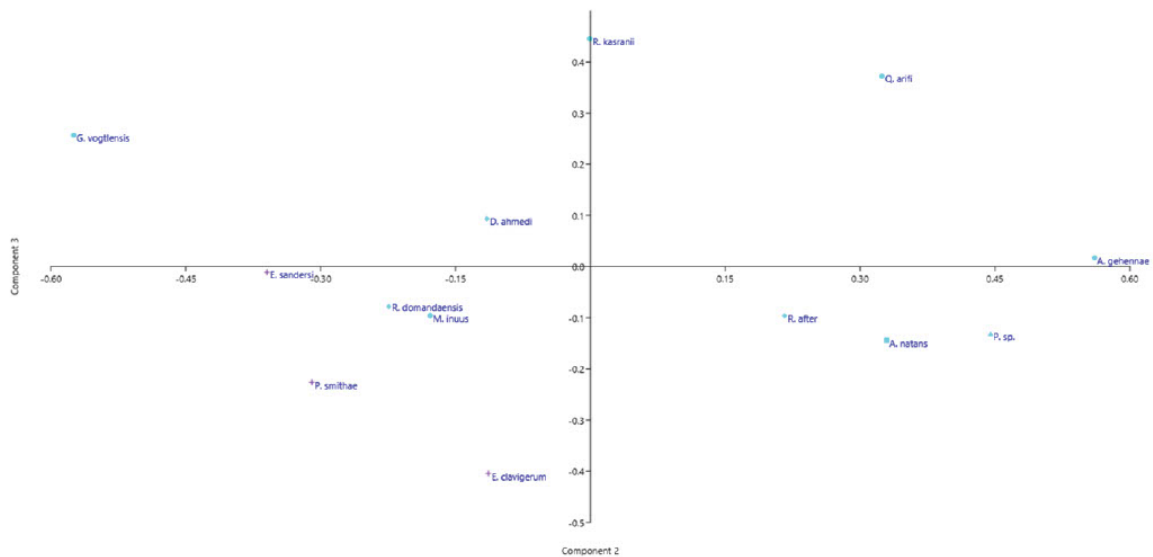


Figure 26 Scatter plot comparing the second and third principal components for distances measured on archaeocete and sirenian pelves. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelves. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

The second and fourth principal components (figure 27) are much different than previous iterations, with *E. clavigerum* being relatively distant from *P. smithae* and *E. sandersi*. *E. clavigerum* is closest spatially to *D. ahmedi*, whereas *E. sandersi* and *P. smithae* lay opposite to *M. inuus* and *R. domandaensis*. The other spatial relationships of the archaeocetes haven't changed significantly.

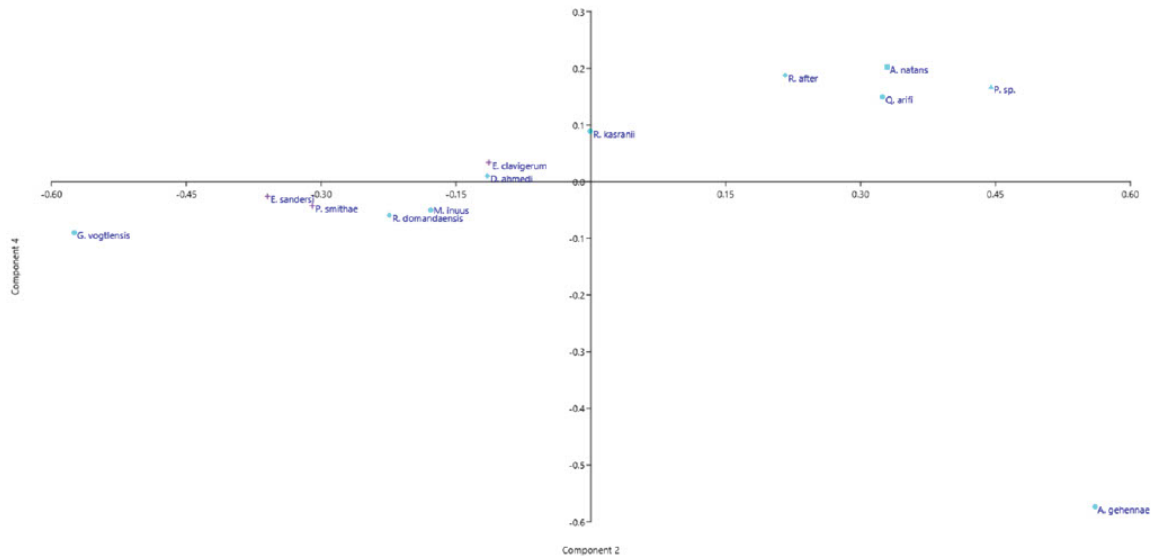


Figure 27 Scatter plot comparing the second and fourth principal components for distances measured on archaeocete and sirenian pelvises. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelvises. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups:

Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

The third and fourth components (figure 28) see the widest spatial spread of the three sirenian taxa. *P. smithae* and *E. sandersi* lay on opposite sides of the closely positioned *M. inuus* and *R. domandaensis*, whereas *E. clavigerum* remains isolated above the x-axis in the upper right corner of the plot. Despite their spread across the fourth component, there is little vertical variation (along the y-axis, or along component 3).

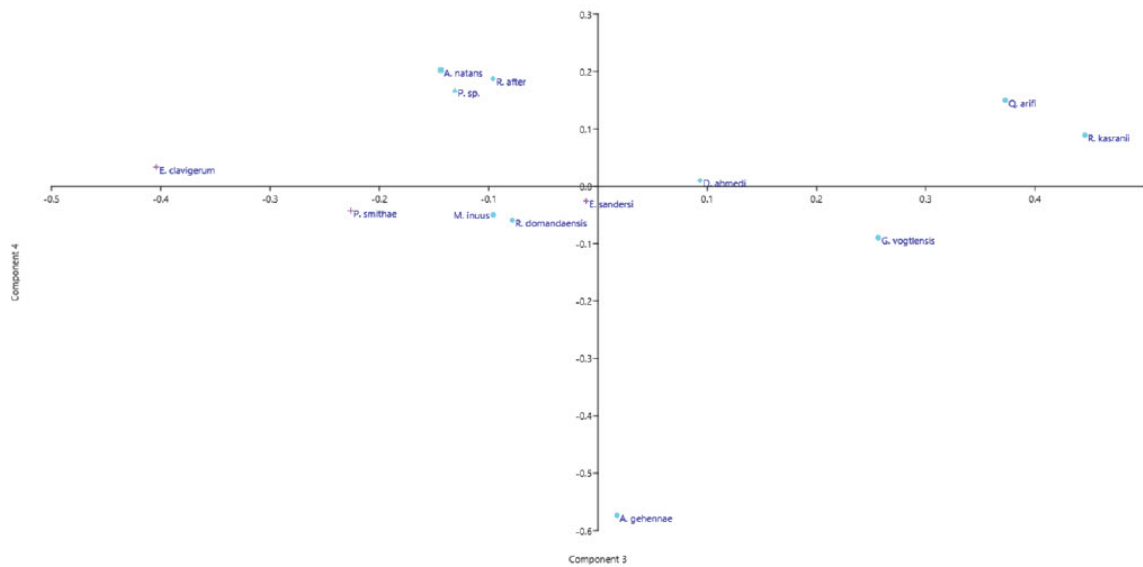


Figure 28 Scatter plot comparing the third and fourth principal components for distances measured on archaeocete and sirenian pelves. Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and sirenian pelves. The light blue color represents archaeocetes and the violet color represents sirenians. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Sirenia (+).

Viewing the loadings (table 6), the first principal component explains much of the positive variation for distances 4 to 5, 5 to 8, and 5 to 10 and some of the positive variation for distance 5 to 7. It also explains some of negative variability for distance 4 to 7. The second principal component makes up most of the positive variation for distances 4 to 7, 7 to 8, 7 to 10, and 9 to 10. It also makes up some of the positive variation for 4 to 8, 5 to 10, 7 to 9, 8 to 9, and 8 to 10. The third principal component makes up most of the positive variation for distances 7 to 9, 8 to 9, and 8 to 10. It also makes up some of the positive variation for distance 9 to 10. The third principal component makes up a lot of the negative variation for distances 4 to 7, 4 to 8, and 5 to 10 and some of the negative variation for distance 4 to 5. The fourth principal component represents most of the positive variation for distance 4 to 7. The fourth principal component makes up most of the variation for distances 4 to 8 and 5 to 7, as well as some of the positive variation for 7 to 9 and 9 to 10. The fourth component also makes up most of the negative variation for distances 4 to 5, 5 to 8, 7 to 8, and 8 to 10.

Table 6 Loadings for all principal components for distances measured on archaeocete and sirenian pelves.

Procrustes Distances	Anatomical Distances	PC 1	PC 2	PC 3	PC 4
4 to 5	narrowest part of the ilial neck to the narrowest part of the ilial neck	0.53836	-0.071905	-0.14524	-0.34261

4 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	-0.11317	0.55604	-0.4455	-0.096935
4 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	-0.052214	0.25277	-0.45161	0.45057
5 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	0.44284	0.020207	-0.086559	0.57355
5 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	0.50511	0.081651	0.05233	-0.22007
5 to 10	narrowest part of the ilial neck to the dorsal margin of the semilunate surface	0.46814	0.11042	-0.16285	0.0016815
7 to 8	ventral margin of the semilunate surface to the anterior margin of the semilunate surface	-0.066127	0.37307	-0.088432	-0.41875
7 to 9	ventral margin of the semilunate surface to the anterior end of the notch	0.069175	0.28934	0.47759	0.25764
7 to 10	ventral margin of the semilunate surface to the dorsal margin of the semilunate surface	-0.065231	0.42935	0.054322	-0.056972
8 to 9	anterior margin of the semilunate surface to the anterior end of the notch	0.071773	0.27967	0.38061	0.024006
8 to 10	anterior margin of the semilunate	0.060753	0.24545	0.33616	-0.10127

	surface to the dorsal margin of the semilunate surface				
9 to 10	anterior end of the notch to the dorsal margin of the semilunate surface	0.044602	0.23829	0.20736	0.19239

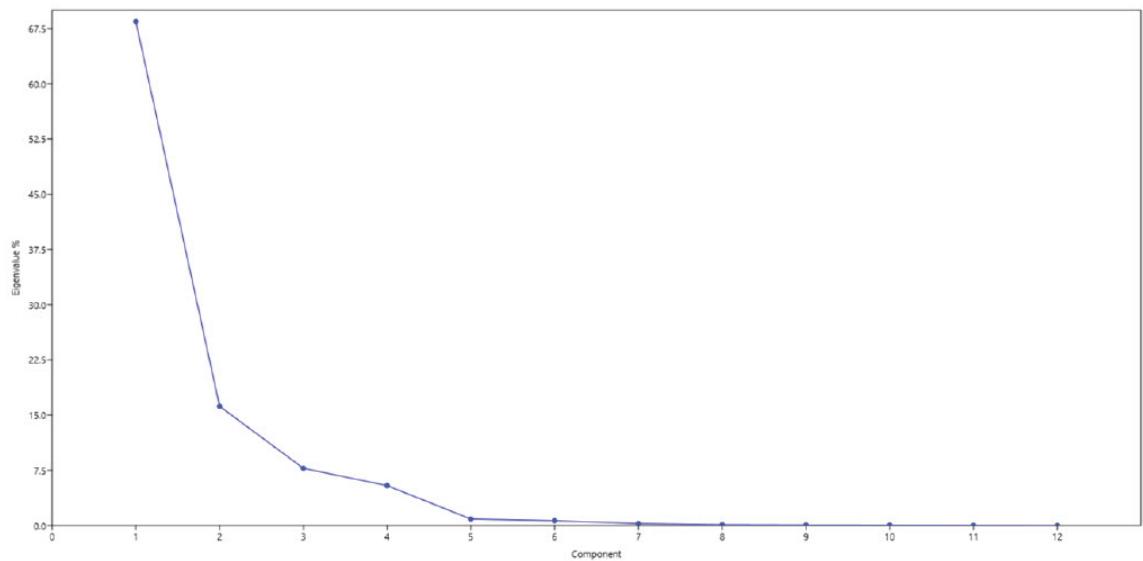


Figure 29 Scree plot showing how much variation is covered in each principal component for distances measured on archaeocete and sirenian pelves.

Archaeocetes & Mustelids

Table 7 Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete and mustelid pelves.

PC	Eigenvalue	% variance
1	0.645659	53.369
2	0.283398	23.425
3	0.120473	9.958
4	0.0730836	6.041

With the fourth set of statistical analyses, principal component analyses are run for the archaeocetes and mustelids. Just as with the previous groups, the same landmark configuration and distances are used. As seen in table 7 and figure 36, the vast majority of the variation is limited to the first four principal components. In this case, the first two components make up about 76% of variability, with the third and fourth components making up another 15%. The scatter plot comparing components 1 and 2 (figure 30) has similar archaeocete groupings, just as with the pinnipeds and sirenians. The mustelids, *Enhydra lutris nereis*, *Lontra canadensis canadensis*, *Mustela putorius*, and *Neogale vision energumenos* loosely occupy the upper left section of the scatter plot. The closest archaeocetes to this loose cluster of mustelids are the closely paired *Pakicetus sp.* and *Ambulocetus natans*. The remaining archaeocetes maintain similar positions compared to previous principal component analyses.

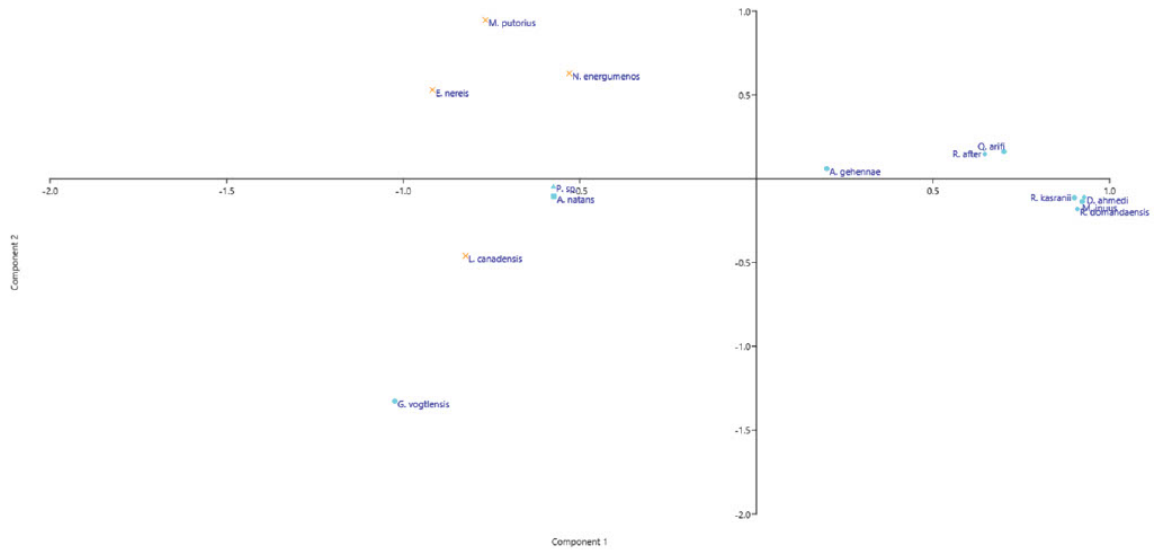


Figure 30 Scatter plot comparing the first and second principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

When comparing the first and third components (figure 31), *M. putorius* and *L. canadensis* lay close together, just below the third component on the left side of the plot. They are spatially close to *P. sp.* and *A. natans*, as with the first two components, however they also nearby to *G. vogtlensis*. *E. nereis* and *N. energumenos* are far both

from each other, and the other two mustelids, with *N. energumenos* occupying the top of the top left corner of the plot. *E. nereis*, on the other hand, is on the bottom of the bottom left corner of the map, opposite *N. energumenos*. This is one of the few instances where *G. vogtlensis* plots close to other taxa, with it being nearby to both *P. sp.*, *A. natans*, and some of the mustelids.

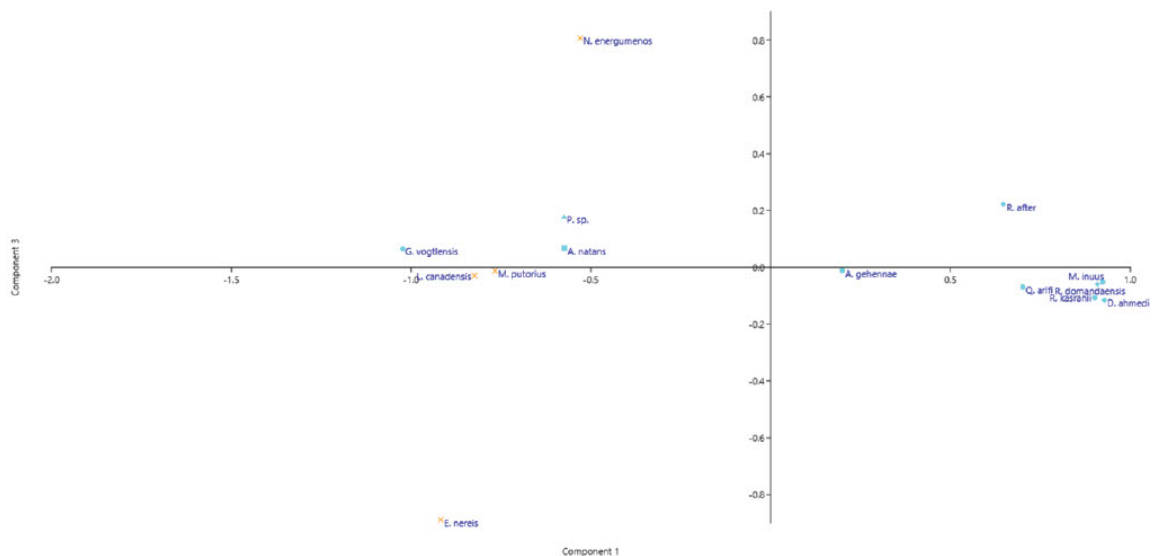


Figure 31 Scatter plot comparing the first and third principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

With the comparison between the first and fourth components (figure 32), *L. canadensis*, *N. energumenos*, and *E. nereis*, all occupy the top left corner of the plot, with no other taxa nearby. While they are all about equidistant, *M. putorius* is isolated in the lower left portion of the plot, with the closest taxa being *G. vogtlensis*, *P. sp.*, and *A. natans*, though all the cetaceans are still distant from the mustelid.

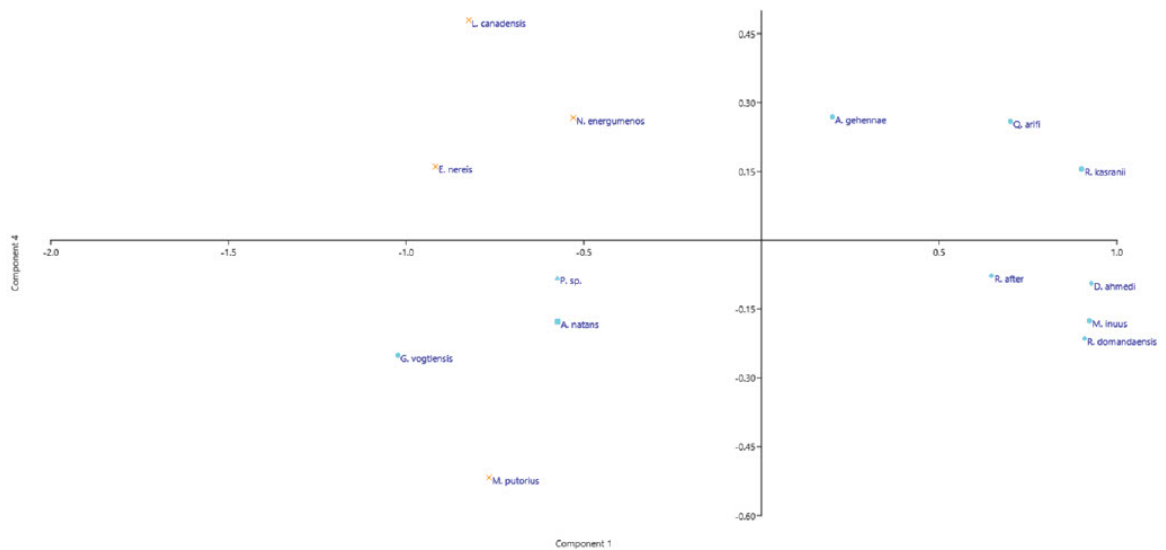


Figure 32 Scatter plot comparing the first and fourth principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

With the comparison of the second and third principal components (figure 33), the biggest changes seen yet become visible. *L. canadensis* is spatially clustered with *M. inuus*, *R. domandaensis*, *R. kasranii*, and *D. ahmedi*. Far away, the other three mustelids lay on the fringes, being separated mostly along the second component. *N. energumenos* lays on the top right corner of the plot, while *E. nereis* is positioned opposite along the bottom right corner, with *M. putorius* medially between them.

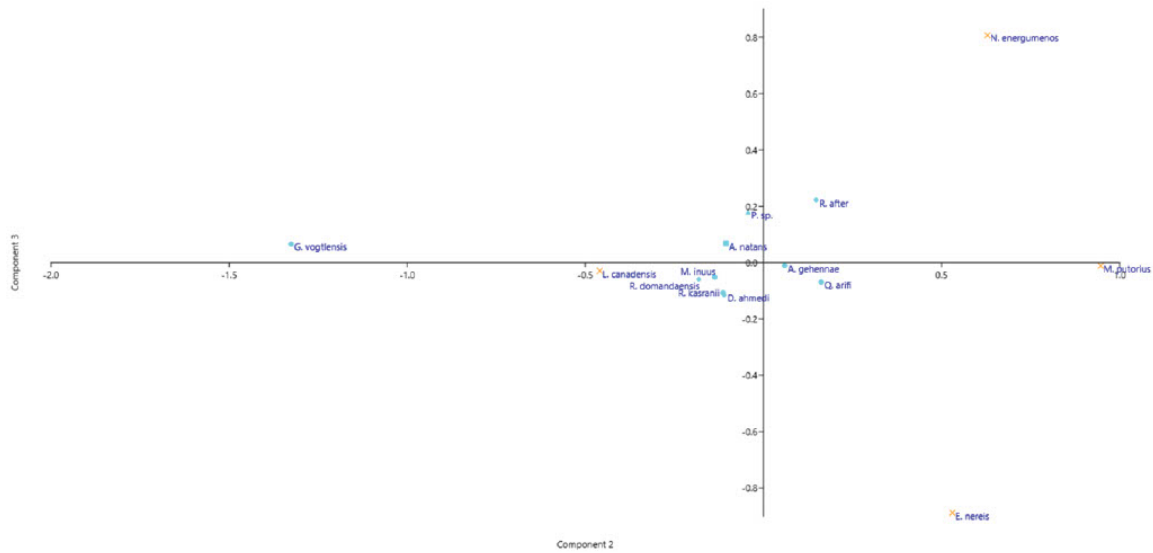


Figure 33 Scatter plot comparing the second and third principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

As with the previous iteration, when comparing the second and fourth components (figure 34), many of the taxa are spatially displaced. *M. putorius* lays opposite *L. canadensis*, with *L. canadensis* being located in the upper left corner of the plot, and *M. putorius* in the lower right corner. *N. energumenos* and *E. nereis* are held tightly together, both occupying the upper right corner of the plot. The nearest archaeocete is *Q. arifi*, however it is still quite a distance from these mustelid taxa.

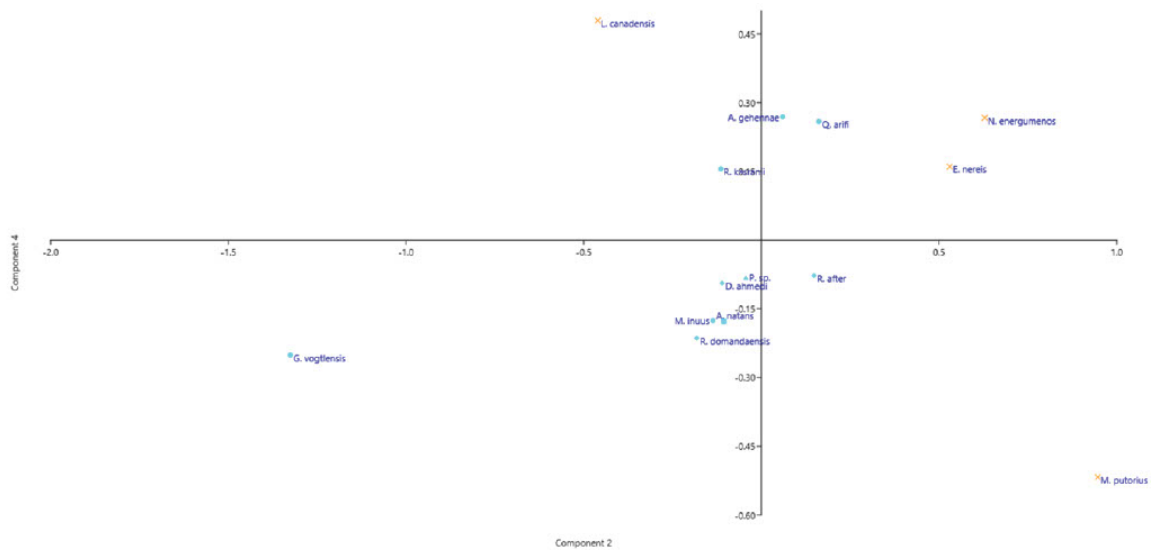


Figure 34 Scatter plot comparing the second and fourth principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

The third and fourth principal components (figure 35) have most taxa centered along the y-axis (component 3). *L. canadensis* and *M. putorius* occupy opposite ends of component three, but have almost no variation across component 4. The opposite is true for *E. nereis* and *N. energumenos*, as both of these taxa are on opposite ends of component four, with almost no change across component 3.

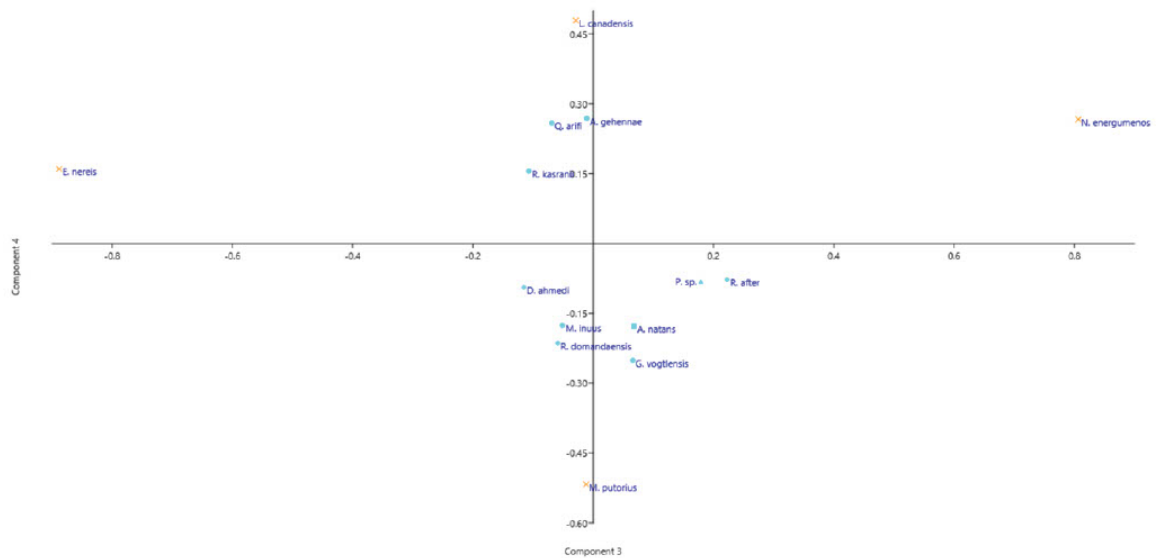


Figure 35 Scatter plot comparing the third and fourth principal components for distances measured on archaeocete and mustelid pelves. The light blue color represents archaeocetes and the orange color

represents mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), and Remingtonocetidae (◆), Mustelidae (X).

When looking at the loadings (table 8), the first principal component explains the majority of the positive variation for distances 4 to 5, 5 to 8, and 5 to 10 and some of the positive variation for distance 5 to 7. It also explains most of negative variability for distances 4 to 7 and 4 to 8, as well as some of the negative variation for distances 7 to 8 and 7 to 10. The second principal component makes up most of the positive variation for distances 4 to 7, 5 to 7, 7 to 8, 7 to 9, and 7 to 10, as well as some of the positive variation for 4 to 8, 5 to 8, and 5 to 10. The third principal component makes up most of the positive variation for distances 4 to 8 and 9 to 10. It also makes up some of the positive variation for distances 4 to 7, 5 to 8, 8 to 9, and 8 to 10. The third principal component makes up a lot of the negative variation for distances 4 to 5, 7 to 8, 7 to 9, and 7 to 10, as well as some of the negative variation for distance 5 to 7. The fourth principal component represents most of the positive variation for distance 8 to 9 and 8 to 10. The fourth principal component also makes up some of the positive variation for distances 4 to 5, 4 to 8, 7 to 9, 7 to 10, and 9 to 10, and most of the negative variation for distances 5 to 7, 5 to 10. In addition, the fourth principal component makes up some of the negative variation for distance 4 to 7.

Table 8 Loadings for all principal components for distances measured on archaeocete and mustelid pelves.

Procrustes Distances	Anatomical Distances	PC 1	PC 2	PC 3	PC 4
4 to 5	narrowest part of the ilial neck to the narrowest part of the ilial neck	0.49776	-0.047071	-0.34753	0.44098
4 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	-0.26889	0.48305	0.21855	-0.14366
4 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	-0.2142	0.33716	0.41549	0.18548
5 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	0.28426	0.48923	-0.19849	-0.351
5 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	0.47629	0.27505	0.30618	0.020119
5 to 10	narrowest part of the ilial neck to the dorsal margin of the semilunate surface	0.47838	0.19642	0.084048	-0.22183
7 to 8	ventral margin of the semilunate surface to the anterior margin of the semilunate surface	-0.18375	0.33355	-0.088432	-0.41875
7 to 9	ventral margin of the semilunate surface to the anterior end of the notch	0.069175	0.28934	-0.31699	0.067637
7 to 10	ventral margin of the semilunate surface to the dorsal margin of the semilunate surface	-0.20905	0.31212	-0.24345	0.2699

8 to 9	anterior margin of the semilunate surface to the anterior end of the notch	0.056649	0.067929	0.26585	0.49456
8 to 10	anterior margin of the semilunate surface to the dorsal margin of the semilunate surface	0.072304	0.021027	0.22477	0.38844
9 to 10	anterior end of the notch to the dorsal margin of the semilunate surface	0.069699	0.079528	0.2043	0.18212

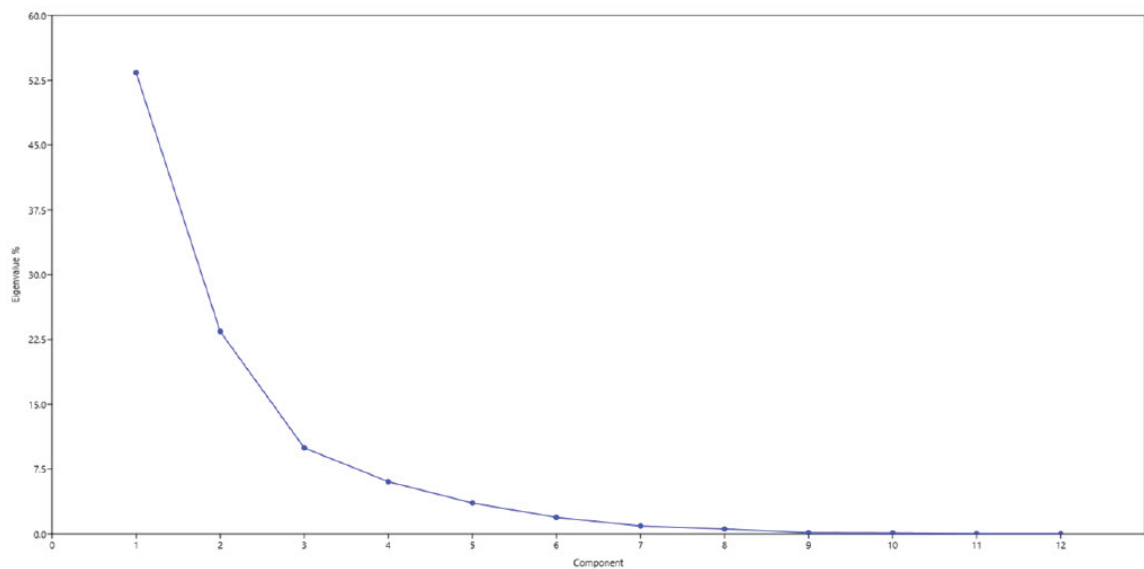


Figure 36 Scree plot showing how much variation is covered in each principal component for distances measured on archaeocete and mustelid pelves.

All Taxa

Table 9 Summary statistics for principal components analysis (PCA) run for distances measured on archaeocete, pinniped, sirenian and mustelid pelves.

PC	Eigenvalue	% variance
1	0.500709	45.807
2	0.203568	18.623
3	0.175904	16.092
4	0.096992	8.873

With the final statistical analysis, a principal component analysis has been run for all of the previous taxonomic groups together: archaeocetes, pinnipeds, sirenians, and mustelids. The same landmark configuration and distances were used. As seen in table 9 and figure 43, the vast majority of the variation is limited to the first four principal components. In this case, the first two components make up about 63% of variability, with the third and fourth components making up another 24%. The scatter plot comparing components 1 and 2 (figure 37) has many of the previous qualities of the other principal component analyses, however their positions relative to cetaceans are more visible. The mustelids group loosely together in the left side of the plot, close to *Pakicetus sp.* and *Ambulocetus natans*, but also to the pinniped *Cystophora cristata*, which is closest to *E. nereis*. Most of the spatial relationship between archaeocetes, pinnipeds, sirenians, and mustelids are similar. *Qaisracetus arifi* and *Rodhocetus kasranii* are close together, as well as *Ryanistes after*, *Dalanistes ahmedi*, *Maiacetus inuus*, and *Remingtonocetus*

domandaensis. The sirenians are grouped closely together nearby to the aforementioned cluster of protocetids and remingtonocetids. The pinnipeds are relatively spread out, with *Odobenus rosmarus* close to the center of the plot, *Pagophilus groenlandicus* at the top center of the plot, and *Pusa hispida* close to *Zalophus californianus* in the top right corner.

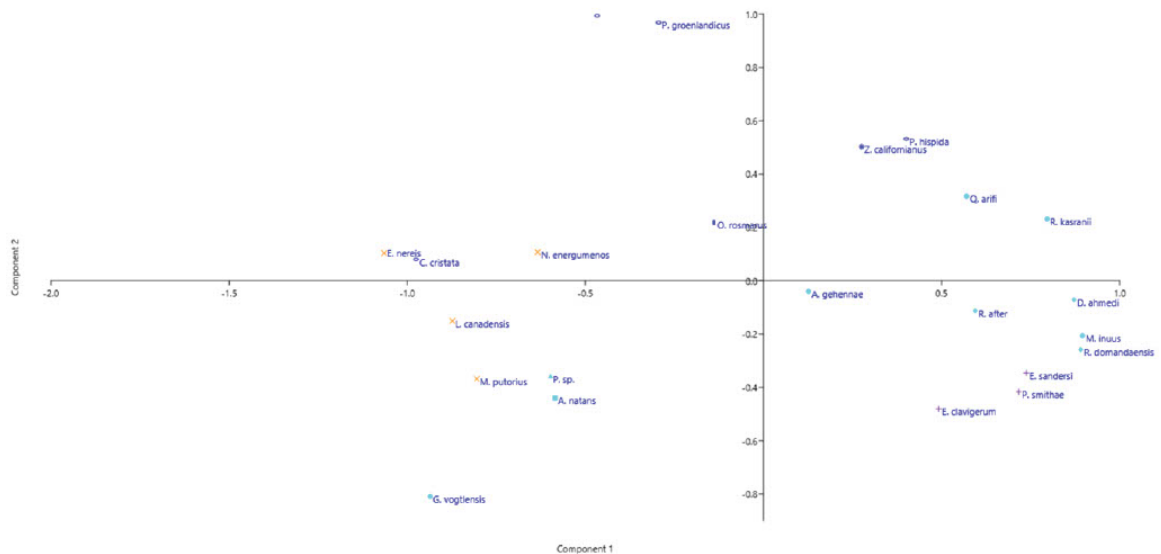


Figure 37 Scatter plot comparing the first and second principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (○), Otariidae (⊗), Odobenidae (▮), Sirenia (+), and Mustelidae (X).

When comparing the first and third components (figure 38), one can see that most of the archaeocetes are held together rather tightly, with the exceptions being *P. sp.* and *A. natans*, which are close together to the left, as well as the isolated *G. vogtlensis*. Most of the mustelids and pinnipeds have changed only slightly in position, with their spatial relationships being maintained. The sirenians have spread out across component 3, with *P. smithae* and *E. sandersi* remaining close together and nearby to the protocetids and remingtonocetids. *E. clavigerum* has migrated above the third component, close to *R. after* and *Q. arifi*.

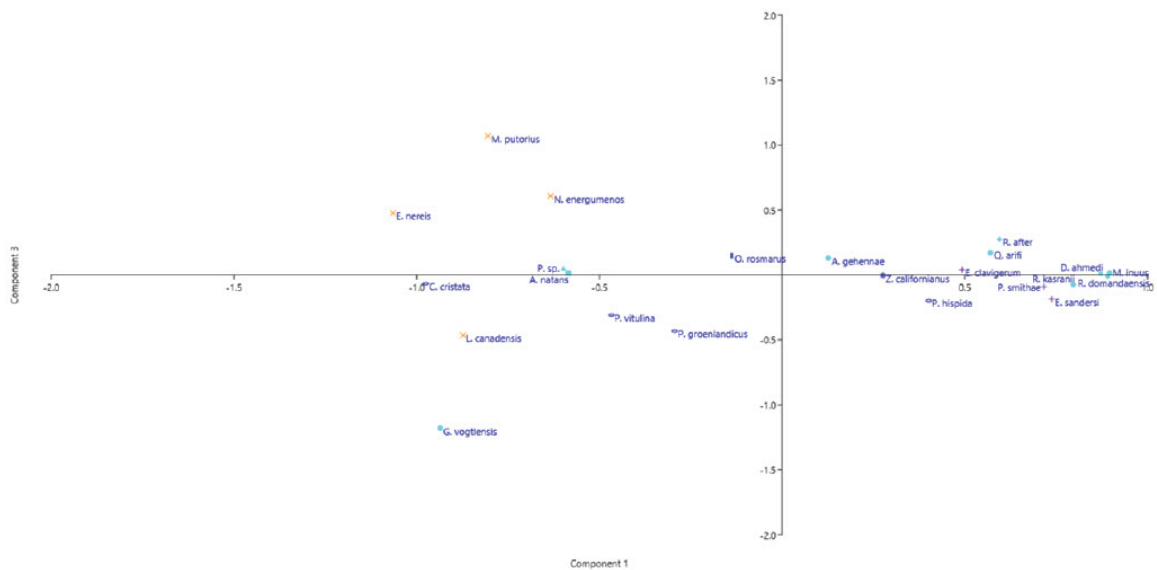


Figure 38 Scatter plot comparing the first and third principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller

taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), Odobenidae (▮), Sirenia (+), and Mustelidae (X).

The first and fourth components (figure 39) for these taxa has a larger spread of both the pinnipeds and mustelids, while the archaeocetes and sirenians have not changed their position drastically. *M. putorius* and *L. canadensis* are close together, and nearby to *G. vogtlensis*. *C. cristata* and *E. nereis* are close in position again, though they are isolated from most other taxa. *N. energumenos* is isolated at the top of the top left corner of the plot. *E. clavigerum* is close to *P. hispida* and *Q. arifi*, while *Z. californianus* is relatively isolated from other taxa.

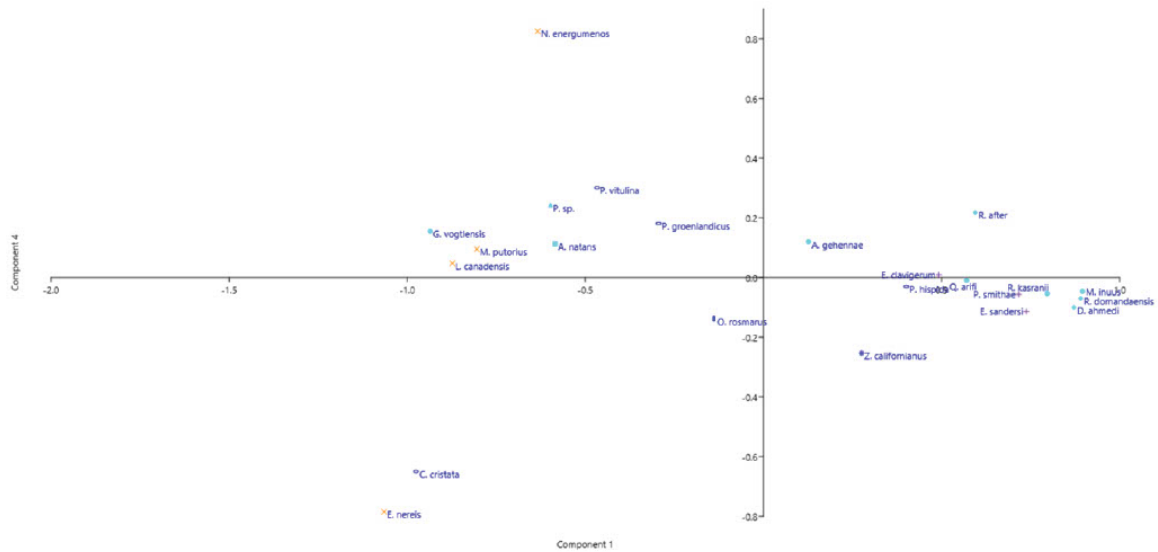


Figure 39 Scatter plot comparing the first and fourth principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), Odobenidae (■), Sirenia (+), and Mustelidae (X).

For the second and third components (figure 40), *N. energumenos* and *E. nereis* are close together, while both *M. putorius* and *L. canadensis* are isolated (though they differ most with component 2, and are similar in component 3). The sirenians are relatively close together, though *E. clavigerum* is closest to *A. natans*. *O. rosmarus* is close to both *R. kasranii* and *Q. arifi*. *G. vogtensis* remains the most isolated of the taxa displayed.

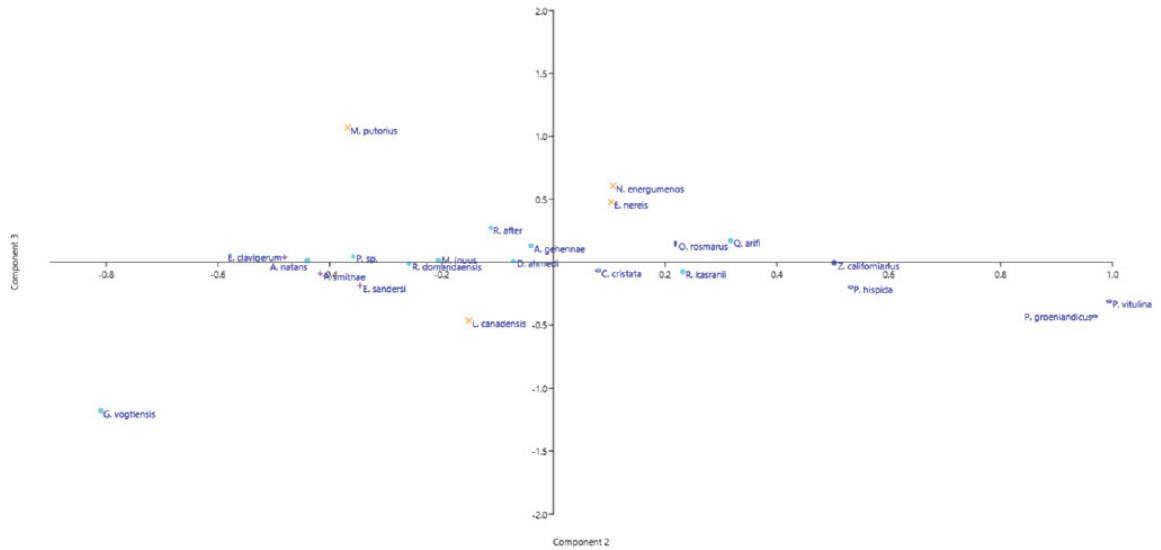


Figure 40 Scatter plot comparing the second and third principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (⊖), Otariidae (✱), Odobenidae (◼), Sirenia (+), and Mustelidae (X).

With the second and fourth components (figure 41), *N. energumenos* and *E. nereis* have some of the most dramatic variability. They are found on opposite ends of component 2, however do not vary significantly in terms of component 4. The opposite is true for *G. vogtensis* when compared with both *P. groenlandicus* and *P. vitulina*. In this case, they vary along component four, but not much at all across component 2. For most taxa, indeed, the variation appears to be horizontal, spread across component 4. *O.*

rosmarus is very close to *R. kasranii*, while *M. putorius* and *L. canadensis* are loosely held amidst protocetids, remingtonocetids, and sirenians.

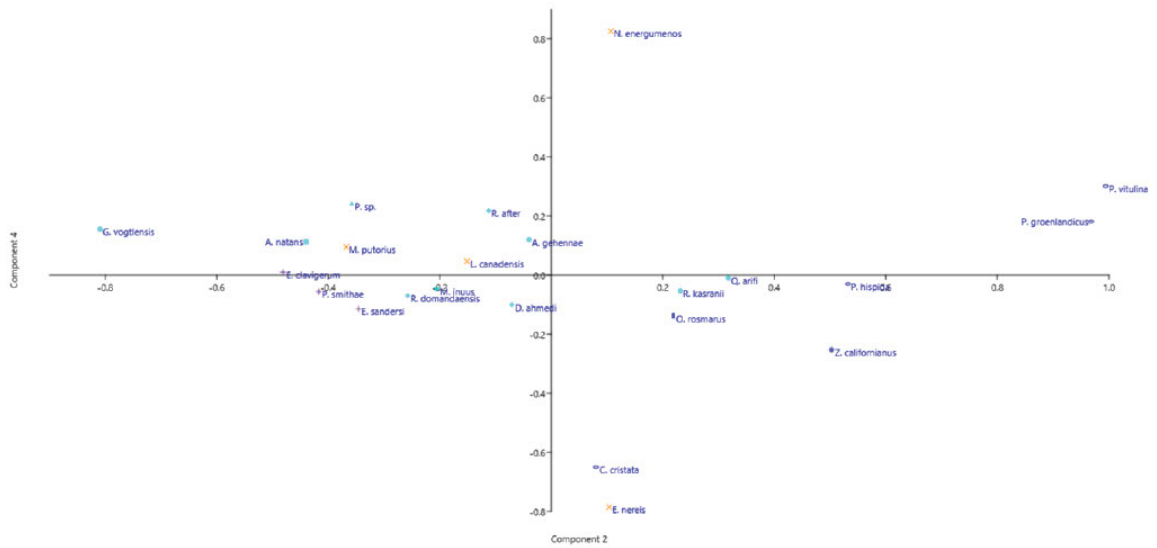


Figure 41 Scatter plot comparing the second and fourth principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (○), Otariidae (⊗), Odobenidae (▮), Sirenia (+), and Mustelidae (X).

The third and fourth components (figure 42) have almost all of the taxa surrounding the central point of the plot. The largest outliers are three of the mustelids, *N. energumenos*, *M. putorius*, and *E. nereis*. *G. vogtensis* also lays at the fringes, though not to the extent of the aforementioned mustelids. Most archaeocetes are close together near

the center, along with the sirenians and pinnipeds. Some pinnipeds, such as *Z. californianus*, *C. cristata*, *P. vitulina*, and *P. groenlandicus*, are relatively close to the archaeocetes and sirenians, but held at more of a distance. *L. canadensis* is closely positioned to *P. groenlandicus*.

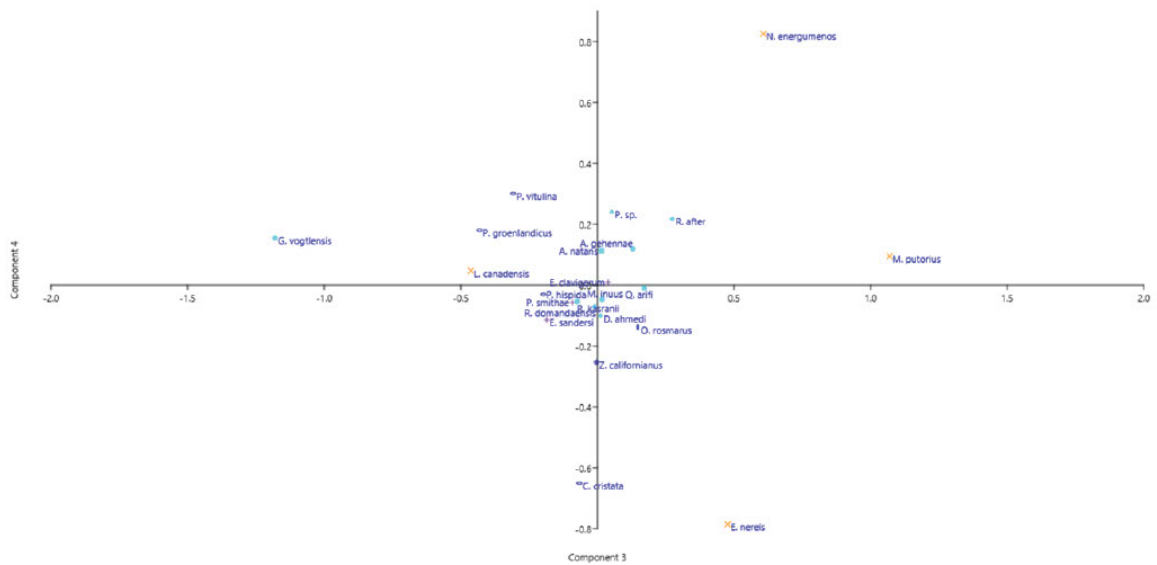


Figure 42 Scatter plot comparing the third and fourth principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves. The light blue color represents archaeocetes, the dark blue pinnipeds, the violet sirenians, and orange mustelids. The shape of each point refers to smaller taxonomic groups: Ambulocetidae (■), Pakicetidae (▲), Protocetidae (●), Remingtonocetidae (◆), Phocidae (○), Otariidae (✱), Odobenidae (■), Sirenia (+), and Mustelidae (X).

Viewing these final loadings (figure 43), the first principal component explains the majority of the positive variation for distances 4 to 5, 5 to 8, and 5 to 10 and some of the positive variation for distance 5 to 7. It also explains most of negative variability for distances 4 to 7, 4 to 8, and 7 to 10, as well as some of the negative variation for distances 7 to 8 and 7 to 9. The second principal component makes up most of the positive variation for distances 7 to 9, 7 to 10, 8 to 9, 8 to 10, and 9 to 10, as well as some of the positive variation for distances 4 to 5, 5 to 7, and 5 to 8. The second component also makes up the most negative variability for distance 5 to 10, and some of the negative variation for distance 4 to 7. The third principal component makes up most of the positive variation for distances 4 to 7, 4 to 8, 5 to 7, and 7 to 8, as well as making up some of the positive variation for distances 5 to 8, 5 to 10, 7 to 9, and 7 to 10. The third principal component makes up a lot of the negative variation for distance 8 to 10. The fourth principal component makes up some of the positive variation for distances 4 to 7, 4 to 8, 5 to 8, 8 to 9, 8 to 10, and 9 to 10, as well as making up most of the negative variation for distances 4 to 5, 5 to 7, 7 to 8, and 7 to 9. In addition, the fourth principal component makes up some of the negative variation for distance 7 to 10.

Table 10 Loadings for all principal components for distances measured on archaeocete, pinniped, sirenian and mustelid pelves.

Procrustes Distances	Anatomical Distances	PC 1	PC 2	PC 3	PC 4
4 to 5	narrowest part of the ilial neck to the narrowest part of the ilial neck	0.45721	0.19218	- 0.078812	- 0.39564
4 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	-0.23434	-0.17424	0.54262	0.31748
4 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	-0.22579	- 0.057967	0.3409	0.23097
5 to 7	narrowest part of the ilial neck to the ventral margin of the semilunate surface	0.24444	0.18989	0.45069	- 0.23794
5 to 8	narrowest part of the ilial neck to the anterior margin of the semilunate surface	0.45901	0.26628	0.23109	0.34978
5 to 10	narrowest part of the ilial neck to the dorsal margin of the semilunate surface	0.50458	-0.25369	0.35029	0.04095
7 to 8	ventral margin of the semilunate surface to the anterior margin of the semilunate surface	-0.22415	-0.02949	0.34678	- 0.35341
7 to 9	ventral margin of the semilunate surface to the anterior end of the notch	-0.16045	0.36564	0.21104	- 0.37205
7 to 10	ventral margin of the semilunate surface to the dorsal margin of the semilunate surface	-0.28982	0.45147	0.14197	- 0.15488
8 to 9	anterior margin of the semilunate surface to the anterior end of the notch	- 0.0038934	0.37365	- 0.010851	0.22593
8 to 10	anterior margin of the semilunate surface to the dorsal margin of the semilunate surface	0.0020251	0.47792	-0.13297	0.3781
9 to 10	anterior end of the notch to the dorsal margin of the semilunate surface	0.004238	0.22719	0.03421	0.16545

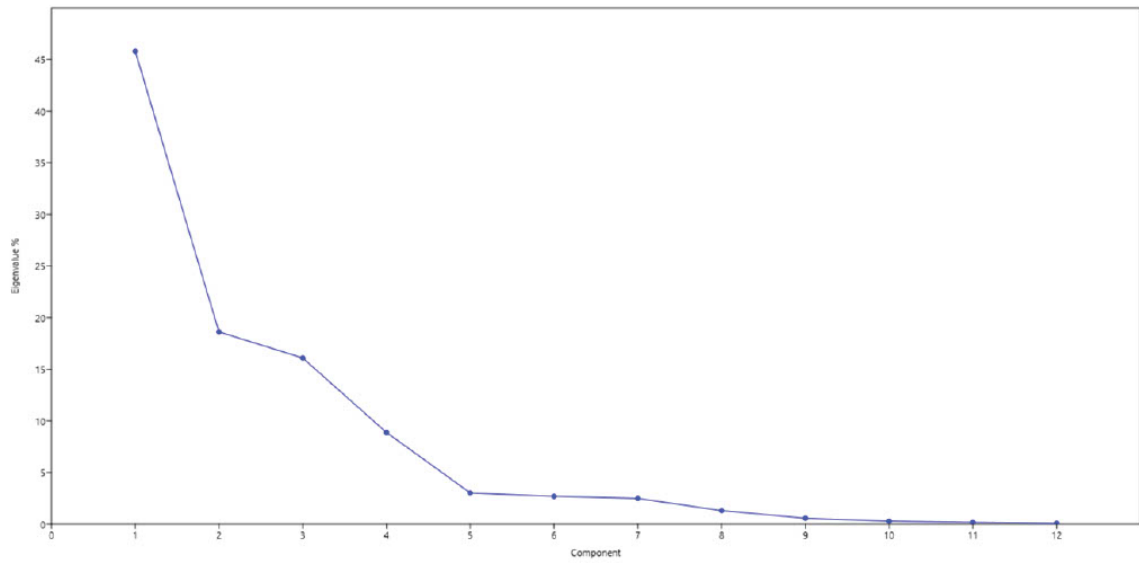


Figure 43 Scree plot showing how much variation is covered in each principal component for distances measured on archaeocete and mustelid pelves.

DISCUSSION

Drivers of Morphological Variation

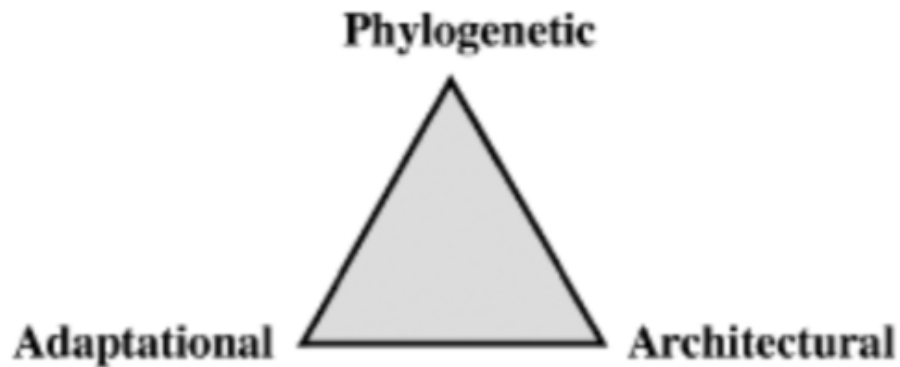


Figure 44 Seilacher's triangle, which depicts the three factors that influence the variability of an organism's character state (Cubo et al., 2008).

One of the most famous frameworks for characterizing the biological features of an organism is known as Seilacher's Triangle (Cubo et al., 2008). This is a ternary diagram, much like the Quartz-Feldspar-Lithics (QFL) or Clay-Sand-Silt geological diagrams, where there are three factors that influence a character state: historical (phylogenetic), functional (adaptational), and structural (architectural) (Cubo et al., 2008). In the case of archaeocetes, I hypothesized that locomotor mode, and thereby the adaptational factor,

plays the biggest role in driving shape change. This would be expectedly followed by historical, and then structural factors, respectively. My initial hypothesis, however, while lent some credence by the results, is much more complex than originally expected. Indeed, specimens that would also be thought to be grouped closely due to their phylogenetic affinities even appear to be missing. Instead, while there are aspects of both adaptation and phylogeny, architecture may play a bigger role than expected. Overall, however, the innominate is just one small part of the postcranial skeleton, with the entire hindlimb and vertebral column being unincluded. My primary hypothesis is that the main driver of shape variability of the innominate is aquatic locomotor mode. My secondary hypothesis is that the main driver of shape variability in the innominate is phylogenetic variability and osteological robustness. I reject both my primary and secondary hypotheses. To receive a proper understanding of what is driving the shape of the innominate, a more expansive look at more postcrania is needed.

Locomotor Mode

In order to provide evidence that certain archaeocetes used a particular swimming mode, they must be compared with extant mammals with known aquatic locomotor modes. While in many cases this does occur, the consistency and proximity of taxa with vastly different aquatic locomotor modes does not always lend support for this. Phocids use the same general dorsoventral undulations to swim, with some slight variations in style between phocid taxa. While some phocids, such as *Phoca vitulina* and *Pagophilus groenlandicus* often plot close together, other phocids plot far away, such as *Cystophora cristata* and *Pusa hispida*. Indeed, *Pusa hispida* is often found positioned closely to

Zalophus californianus, despite having completely different locomotory modes. Despite this, many of the phocids plot far from each other. *O. rosmarus* is often found centrally, though it is more often spatially related to phocids, such as *C. cristata*. With odobenids mostly using their hindlimbs and spine to dorsoventrally undulate, they would expectedly be more similar to phocids in innominate shape, since they share similar locomotor modes.

With archaeocetes, one would expect to find protocetids and remingtonocetids associated with lutrines, since they are hypothesized to be pelvic paddlers and dorsoventral undulators. This mostly is not the case, with protocetids and remingtonocetids being more closely positioned with sirenians, with the occasional phocids. Lutrines may have a strong phylogenetic signal (e.g. with other carnivorans) to the point where it overwhelms the functional signal. It is a possibility that previous authors have misinterpreted the locomotory styles of protocetids and remingtonocetids. Phocids may make sense, since they too dorsoventrally undulate, and thus may have similar shaped innominata. The spatial relationship with sirenians, however, is most predominate. With only *P. smithae* possessing hind limbs, the idea that these sirenians' innominata are similar in shape to those of archaeocetes is very unexpected. Sirenians are much more advanced swimmers, with dungongids like *Eotheroides* being efficient dorsoventral oscillators. Thus, while one might expect them to group closely with modern, crown cetaceans, this grouping with hindlimb-powered archaeocetes must be due to something other than locomotor mode. *P. sp.* and *A. natans* are often found in close association with *L. canadensis*, though the latrine *E. nereis* is never nearby and

usually isolated. This could suggest that, as the aquatic locomotion of *A. natans* may actually bear some similarity to otters (Gingerich, 2003). While there are some cases where taxa with similar or expectedly similar locomotor modes plot closely, the majority of cases indicate the opposite. It is unlikely that locomotor mode is the main driver of shape variability of innominata.

Phylogeny

To understand whether phylogeny is a driving factor of variability in shape, one would expect closely related taxa to plot closely to one another, while distantly related taxa would plot far from each other. Based on this idea, some spatial relationships suggest that phylogeny may drive shape variation. Relationships, such as those seen between *A. natans* and *P. sp.* and between the majority of protocetids and remingtonocetids suggest that there is a similarity in overall shape of these innominata. While it is likely phylogeny plays a role, with *A. natans* and *P. sp.* being close, some other results indicate that the drivers are more complex. One would expect all of the protocetids to group together, and all of the remingtonocetids to group together. Instead, there is a clustering of the two together, sometimes with remingtonocetids being closer to protocetids than to other remingtonocetids. For instance, in most plots, *R. after* and *Q. arifi* often plot very closely, and *M. inuus* and *R. domandaensis* are even more closely associated and more often. *Aegicetus gehennae* and *Georgiacetus vogtlensis* are often found isolated from other archaeocete taxa, often found more closely related to pinnipeds or mustelids. This issue extends itself to other taxonomic groups as well. Mustelids show the greatest spread, with multiple taxa, such as *E. nereis*, plotting far from mustelids and

closer to pinnipeds or archaeocetes. Pinnipeds, too, are spread broadly, with some closely related phocids plotting far from each other, where others plot close together. Sirenians tend to plot very close together, however, though the two species of *Eotheroides* plot further away, with *E. sandersi* and *P. smithae* more commonly being found in association. Based on this information, it is unlikely that the majority of variation is explained by phylogenetic affinity, and rather a different driving factor must be at play.

Robustness

While neither locomotor mode nor phylogeny appear to be the main driver of shape change of the innominate, the robustness and structure of the bone itself may be representative of that change. Based on the loadings, it appears, in most cases, that many taxa are plotted closely based on the width of the ischial neck and lengths along the ischium. In other words, taxa with short ischia and wide ischial necks plot close together, while those with longer ischia and narrower ischial necks plot away from them. Semi-aquatic and aquatic mammals tend to have more robust hindlimbs and pelvic girdles (Williams, 1989). Despite all of this information, there is not enough evidence to prove that robustness is the main and only factor in explaining shape variation of the innominate. While it is likely that robustness plays a more significant role than phylogeny or locomotor mode, there are still unknown factors at play.

CONCLUSIONS

Cetaceans are one of the most unique groups of mammals, and one of the best documented cases of the transition from a terrestrial lifestyle to a obligately aquatic one. To better understand this transition, one must be able to characterize how these mammals moved as they swam through the water. By comparing the most basal archaeocetes with the most derived ones, and comparing these taxa to extant marine mammals, their aquatic locomotion could be understood. The best way to understand this locomotory evolution is looking at the part of the body that powers these animals through the water. The ilial section of the innominate, with its supporting the hind limb, and thus much of aquatic locomotion, was the best option to understand the land to sea transition. By characterizing the shape change of archaeocete innominata, one could understand factors what drove their diversification. Through this study, mounting evidence has shown that aquatic locomotory mode was unlikely to be the main driver of innominate shape change for archaeocetes. Even secondary factors, such as phylogeny and robustness, did not fully explain the variation. I reject both my primary and secondary hypotheses, with aquatic locomotor style, phylogenetic affinity, and osteological robustness being insufficient in explaining the shape variability of the innominate. The null hypothesis, that other factors other than the aforementioned three are the main drivers of variability, is probably true. The other factors maybe ecology, however more factors may be revealed upon further

research of archaeocete postcrania. The best way to get a better understanding of this variability would be to look at other postcrania that contribute to aquatic locomotion. The innominate is only one segment in the larger concept of locomotory evolution, and the hind limb and vertebral column must be evaluated in conjunction to uncover the source of shape variability.

APPENDIX



Figure 45 Ventral view of 3D model of the left innominate of *Aegicetus gehennae* (CGM 60584), produced by the University of Michigan Paleontology Collections.

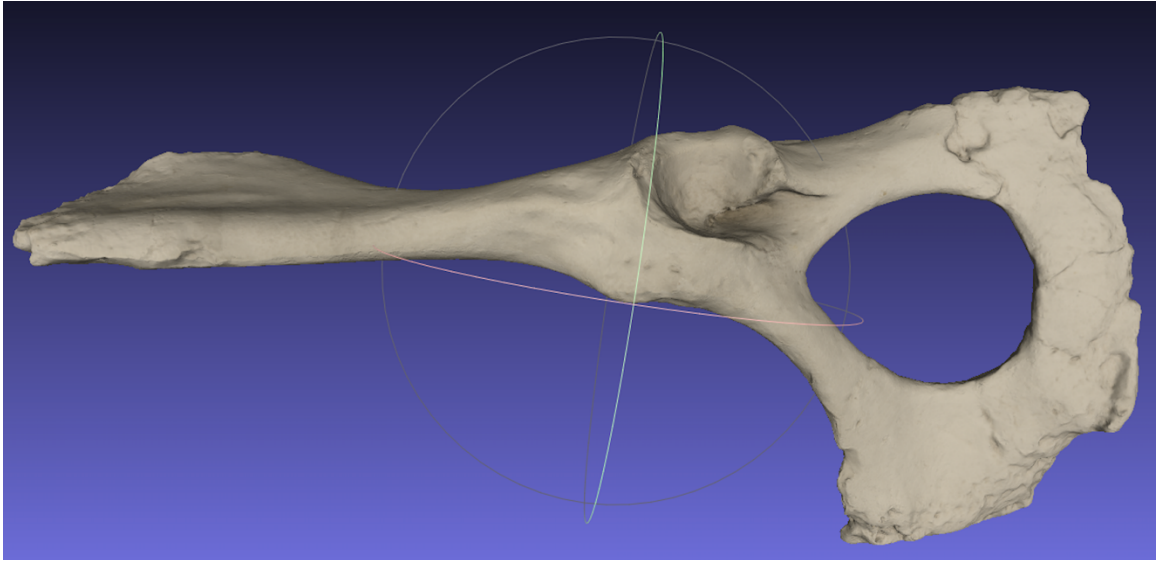


Figure 46 Ventral view of 3D model of the left innominate (cast) of *Georgiacetus vogtlensis* (GSM 350), produced at the University of Michigan Paleontology Collections during the research trip.

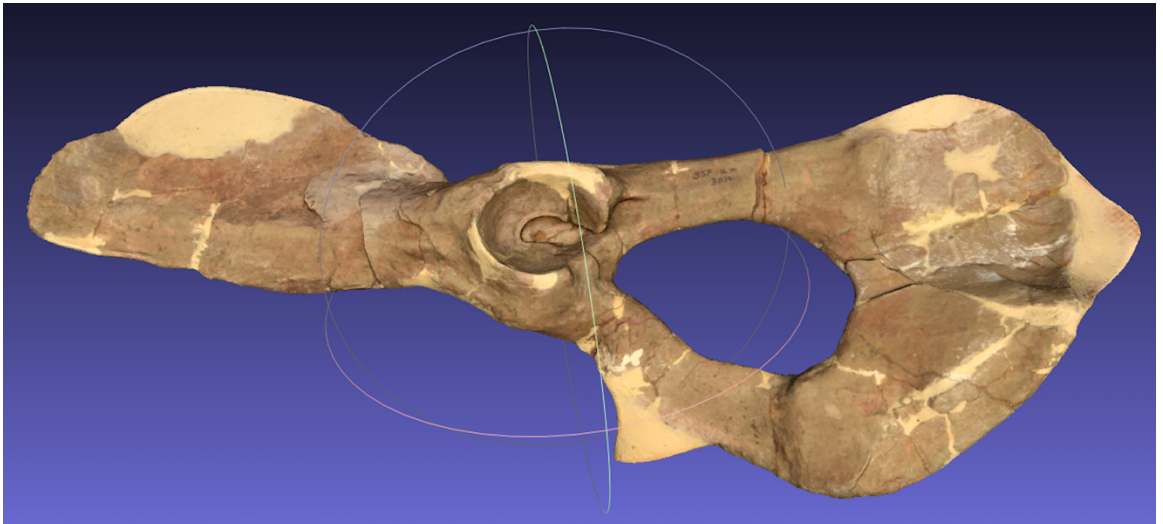


Figure 47 Ventral view of 3D model of the left innominate of *Rodhocetus kasranii* (GSP-UM 3012), produced by the University of Michigan Paleontology Collections.

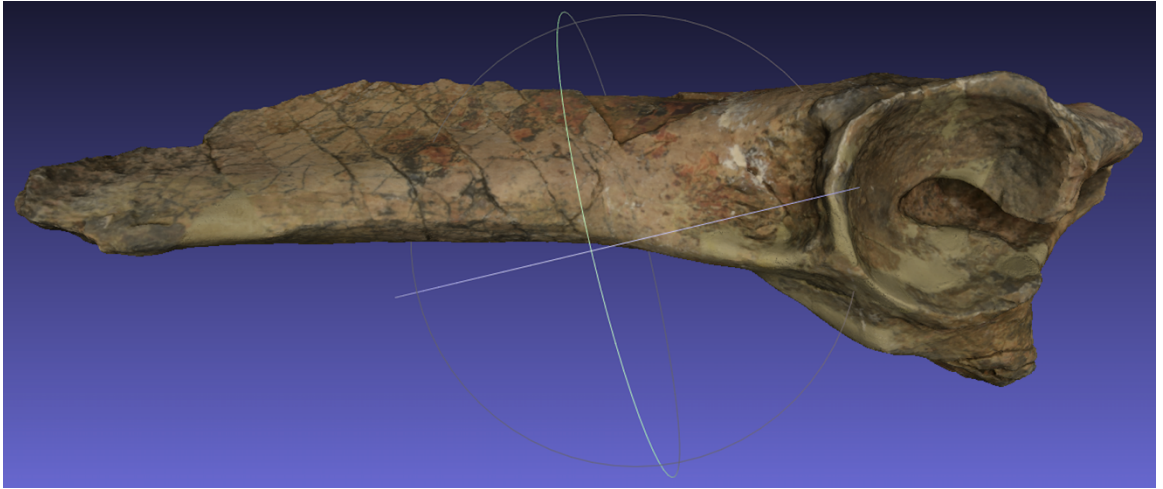


Figure 48 Figure 48: Ventral view of 3D model of the left innominate of *Dalanistes ahmedi* (GSP-UM 3106), produced at the University of Michigan Paleontology Collections during the research trip.

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