**SKELETAL MORPHOLOGY AND EVIDENCE FOR SWIMMING IN A FOSSIL STEM PINNIPED,
PUIJILA DARWINI, FROM THE CANADIAN HIGH ARCTIC**

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ABSTRACT

Puijila darwini is a new genus of fossil carnivore discovered in sediments of the Haughton Formation within the Haughton impact crater on Devon Island, NU (75°N). A previous phylogenetic analysis identified *Puijila* and the Oligocene fossil *Potamotherium vallentoni* as stem pinnipeds (seals, sea lions, walrus). Unlike extant pinnipeds, *Puijila* did not have flippers, but shows evidence of webbed manus and pes. *Puijila* has limb proportions and a long tail which are more reminiscent of terrestrial carnivores. *Puijila* is an important morphological intermediate between modern pinnipeds and their terrestrial ancestors and can provide insight into the early land-to-sea transition of the group. A comparative description of the forelimb indicated *Puijila* was more postcranially specialized for swimming than modern otters (lutrines), but less specialized than its fossil relative *Potamotherium*. The forelimb specializations of *Puijila* provide evidence that the limb may have been used differently during swimming than those of otters. Tetrapod lineages that become secondarily aquatic often display specializations in their internal bone structure that accompany this transition. These specializations can be understood in ancestral pinnipeds, such as *Puijila*, by examining the relationship between bone microstructure and swimming behaviour in their extant relatives, Arctoidea (bears, weasels, pinnipeds etc.). Bone microstructure parameters and swimming behaviour and body mass were compared using phylogenetically independent contrasts. Swimming behaviour and body mass were positively correlated. Bone microstructure showed evidence of correlated evolution only with body mass, indicating

that body mass is the best predictor of swimming behaviour in arctoids. Linear discriminant function analysis supported the observations made from the forelimb description that *Puijila* was semi-aquatic.

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INTRODUCTION

Puijila darwini is a genus of fossil carnivore discovered in 2007 in the Canadian High Arctic. The genus is represented only by the holotype specimen that originates from Early Miocene lacustrine sediments in the Haughton impact crater on Devon Island, Nunavut (Fig. 1). Rybcyzinski et al. (2009) described the specimen and performed a phylogenetic analysis in which *Puijila* grouped with a known fossil stem pinniped. The analysis and description focused on cranial characters, but also made general observations about its postcrania. Unlike modern pinnipeds, *Puijila* lacks flippers, retains a long tail and longer limbs of a terrestrial form. It also has skeletal specializations, such as a large manus and pes, flattened phalanges and shortened ilium, which may be indicative of swimming. It appears to be the least postcranially specialized for swimming of the stem pinnipeds included in the phylogenetic analysis. The early evolution of pinnipeds is not well represented in the fossil record and therefore, *Puijila* represents a crucial example of a transitional form between modern pinnipeds and their terrestrial ancestors. Describing the musculoskeletal and microstructural specializations of the postcrania of *Puijila* in more detail can help to better understand how this animal swam and provide insight into the evolution of pinnipeds from a land to sea habitat.

Previous Research

Since conquering the land during the late Carboniferous, tetrapods have become secondarily aquatic multiple times (Carroll, 1988; Uhen, 2007; Canoville and Laurin, 2010). Within reptiles, birds and mammals, there are many examples of fossil and

FIGURE 1. A, Reconstruction of the holotype skeleton of *Puijila darwini*, NUFV-405, preserved bones are pictured in yellow (modified from Mark A. Clinger in Rybczynski et al., 2009); B, reconstruction of *Puijila darwini*, resting on a rock near the lake shore (image by Brad McFeeters); C, Map of the Canadian High Arctic, Devon Island shaded in black (modified from Rybczynski et al., 2009); D. Map of Devon Island, circle indicates the location of the Haughton Impact Crater where *Puijila darwini* was discovered, (from Rybczynski et al., 2009).

modern taxa, descended from terrestrial lineages, which now occupy freshwater or marine habitats (Howell, 1930; Carroll, 1988; Uhen, 2007). Within Mammalia specifically, there are multiple lineages which are considered aquatic, some of which occupy a strictly marine habitat (Howell, 1930; Nowak, 1991, 2003; Uhen, 2007). The modern marine mammals are typically considered to include Cetacea (dolphins, porpoises, whales), Sirenia (sea cows, dugongs), Pinnipedia (seals, sea lions, walrus), *Enhydra lutris* (sea otter), *Lontra felina* (marine otter) and *Ursus maritimus* (polar bear) (Nowak, 2003). Certain recognizable morphological changes usually accompany the transition of a lineage from a terrestrial to an aquatic existence. The characteristics including a short, robust humerus and femur, elongated digits of the manus and pes and the development of webbing on the feet, help to reduce drag and increase thrust and stability while in the water (Fish, 1996; Uhen, 2007). In marine mammal lineages, modifications to the feeding apparatus to support a diet derived from the water, tend to precede these morphological specializations to aquatic life. This may indicate feeding ecology was a key factor driving the marine mammals' return to the water. In order to overcome the challenges posed by an aquatic existence, a variety of mechanisms and evolutionary pathways were employed (Uhen, 2007).

For some groups of marine mammals, the transition from a terrestrial to an aquatic lifestyle is well represented in the fossil record. The origins of cetaceans can be traced using morphological and molecular evidence to within artiodactyls and the fossil remains of *Indohyus* have provided evidence for the raoellids as their sister group

(Thewissen and Williams, 2002; Thewissen et al., 2007; Uhen, 2007). The fossil record documents their evolutionary transition from terrestrial quadrupedal pakicetids, to semi-aquatic ambulocetids, to completely aquatic fossil and modern cetaceans (Thewissen and Williams, 2002). Geological and isotope evidence has provided further evidence on the ecology of the intermediate forms, suggesting the ancestral cetaceans first occupied freshwater habitats and then transitioned to estuarine and coastal waters, before becoming fully marine (Thewissen and Williams, 2002; Clementz et al., 2006; Thewissen et al., 2007). Other marine mammals have equally well represented links to their terrestrial ancestors. *Pezosiren portelli*, a middle Eocene, semi-aquatic, quadrupedal sirenian has provided insight into the early evolution of this lineage. Isotopic evidence suggests the earliest sirenian ancestors evolved directly into a marine habitat and sea grass diet without occupying a freshwater environment (Domning, 2001; Clementz et al., 2006).

Among marine mammals, the early evolution of Pinnipedia remains the most elusive. Historically, there has been debate whether the group is monophyletic or diphyletic (McLaren, 1960; Tedford, 1976; Berta and Wyss, 1994; Sato et al., 2006; Higdon et al., 2007). Molecular and morphological studies that support a monophyletic origin for pinnipeds have disagreed on whether Musteloidea (weasels, badgers, skunks, raccoons, otters etc.) or Ursidae (bears) is the sister group to the clade and the earliest fossil record of the lineage remained sparse (Berta and Wyss, 1994; Lento et al., 1995; Flynn et al., 2005; Arnason et al., 2006; Sato et al., 2006; Higdon et al., 2007). Multiple

molecular phylogenetic studies have supported that pinnipeds diverged from a single common ancestor based on the use of at least 5 different nuclear DNA, 3 different mitochondrial DNA loci and amino acid sequences, and the majority of those studies identified musteloids as their sister group (Wyss and Flynn, 1993; Berta and Wyss, 1994; Flynn et al., 2005; Fulton and Strobeck, 2006; Sato et al., 2006; Finarelli, 2008). However, our understanding of the appearance and ecology of their earliest ancestors remains lacking, an understanding which would provide insight into their early evolution and their land to sea transition.

Previously, *Enaliarctos* was widely accepted as the most basal fossil pinniped and considered the sister taxon to all other pinnipeds. Yet, *Enaliarctos* is a fully marine, flippered animal (Berta et al., 1989; Berta and Ray, 1990) and so provides little information about the pinniped's evolution from a terrestrial form. *Puijila darwini* bridges this morphological gap in the pinniped fossil record and may provide insight into the transitional period of the group's evolution (Rybczynski et al., 2009).

In the phylogenetic analysis of Rybczynski et al. (2009), *Puijila* was grouped in a clade with *Amphicticeps shackelfordi*, *Potamotherium vallentoni* and the stem pinniped *Enaliarctos mealsi* (Tedford, 1976; Berta et al., 1989; Rybczynski et al., 2009). Of these taxa, *Puijila* appears to be the best candidate as a representative of the pinnipeds' earliest shift towards an aquatic life. The Asian arctoid *Amphicticeps* was identified as the most basal within the clade, but it is only known from cranial elements and so does not provide clues to its level of postcranial aquatic specialization. The European

Oligocene mammal *Potamotherium* is not unanimously considered to be a pinniped. It was originally described by Savage (1957) as a highly specialized lutrine, though even in his original description Savage frequently stated many of its postcranial specializations as being reminiscent of the seal, *Phoca*. Subsequently, *Potamotherium* has been classified as a stem musteloid, an arctoid of unknown affiliation, an oligobunine and a pinniped (Wolsan, 1993; Wyss and Flynn, 1993; Wang et al., 2005; Finarelli, 2008; Rybczynski et al., 2009). Both *Potamotherium* and *Puijila* have limb proportions that are closer to terrestrial musteloids than pinnipeds, lack flippers and retain a long tail, but *Puijila* appears to have less reduction and specialization of the proximal elements of its forelimb (Savage, 1957; Rybczynski et al., 2009). Therefore, regardless of its affiliations, *Potamotherium* has more specialized postcrania than *Puijila*, suggesting *Puijila* is a closer link to the terrestrial ancestors of pinnipeds (Savage, 1957; Rybczynski et al., 2009).

Puijila has already provided interesting insight into pinniped evolution. Its discovery in the High Arctic provides support for the hypothesis of an arctic origin for pinnipeds. Its discovery in lacustrine sediments, coupled with the discovery of other proposed stem pinnipeds, such as *Potamotherium* and the Asian taxon *Semantor*, in freshwater sediments, provides evidence for a freshwater stage in pinniped evolution (Orlov, 1933; Tedford, 1976; Rybczynski et al., 2009).

In addition to the external musculoskeletal specializations required for life in the water, it has been suggested that changes to internal bone microstructure would also accompany a lineage's transition into an aquatic habitat (Wall, 1983; Stein, 1989; Fish

and Stein, 1991; Girondot and Laurin, 2003; Laurin et al., 2004; Cubo et al., 2005; Germain and Laurin, 2005; Laurin et al., 2006; Gray et al., 2007; Krilloff et al., 2008; Houssaye, 2009; Canoville and Laurin, 2010). These modifications to bone microstructure are related to bone density (Wall, 1983). Increased bone density is associated with overall body density; this would be beneficial to animals which forage under the water, as it would offset the natural buoyancy of the animal's body and facilitate diving (Wall, 1983; Stein, 1989; Domning and Debuffrenil, 1991; Fish and Stein, 1991). Increase in bone density (= compactness) can be achieved through "thickening" cortical bone and reducing the size of the medullary cavity within the limb bone, or by thickening the trabecular struts in the spongy bone (Wall, 1983; Houssaye, 2009). Increased bone compactness has been observed in aquatic and semi-aquatic mammals such as beavers, sea otters, ancestral whales and sirenians (Wall, 1983; Stein, 1989; Domning and Debuffrenil, 1991; Fish and Stein, 1991; Houssaye, 2009). I investigated the relationships of bone microstructure, swimming behaviour and body mass within Arctoidea (bears, pinnipeds, weasels, skunks, badgers etc.) that are the extant relatives of *Puijila*. I assessed whether bone microstructure is a good predictor of swimming behaviour in arctoids in order to attempt to predict the swimming behaviour of *Puijila* from its long bone compactness. This aspect of the thesis is presented in the second chapter.

Geological Setting and Paleoenvironmental Inferences of the *Puijila darwini* locality

Puijila darwini was discovered in lacustrine sediments of the Houghton Formation within the Houghton Crater on Devon Island, in the Territory of Nunavut (Rybczynski et al., 2009). The Houghton Crater (75°22' N, 89° 40' W) is a nearly circular impact structure situated in Lower Ordovician to Upper Silurian dolomite and limestone target rocks (Frisch and Thorsteinsson, 1978; Hickey et al., 1988). The raised crater rim is nearly 16 km in diameter, whereas the entire impact structure reaches ~23 km in diameter (Hickey et al., 1988; Osinski et al., 2005). Previously classified as a diapiric structure, the “Houghton dome” was identified as an impact crater in 1972 based on the abundance of shatter cones within the crater (Frisch and Thorsteinsson, 1978; Hickey et al., 1988; Osinski et al., 2005).

The Houghton impact crater was initially dated at 22.4 ± 1.4 Ma based on fission track dating (Omar et al., 1987). Subsequent studies in 1988 and 2005, both using ^{40}Ar - ^{39}Ar radiometric dating, obtained conflicting results of the ages 23.4 ± 1 Ma and 39 ± 2 Ma respectively (Jessberger, 1988; Sherlock et al., 2005). The lacustrine sediments within the crater have been estimated to possibly range in age from late Oligocene to middle Miocene, based on ostracod, plant and vertebrate fossil material, with a more specific estimate of an age of early Miocene (~20mya) (Whitlock and Dawson, 1990).

The unconsolidated, intra-crater sediments of the fossiliferous Houghton Formation are intermittently exposed over an area of 8.62 km^2 and have a maximum thickness of 48 m (Hickey et al., 1988; Whitlock and Dawson, 1990; Osinski and Lee,

2005). The formation is separated into six geographically separate areas; the largest and most fossiliferous portion is crossed by West Rhinoceros Creek and Rabbit Run Creek (Osinski and Lee, 2005). The Haughton Formation's lacustrine sediments are erosional material from the Silurian aged dolomites and limestones of the Allen Bay Formation (Hickey et al., 1988; Osinski and Lee, 2005). The Haughton Formation itself is composed of unconsolidated dolomitic silt-rich muds, with a minor component of dolomitic sand ranging in colour from pale grey to yellow-brown.

The *Puijila* site is located within the active layer above the permafrost. Sediments at the site were observed during excavation to be highly cryoturbated. Throughout the site the cryoturbation was manifested as pockets of grey silt and clay interspersed within yellow-brown sands, destroying the lateral continuity of the original bedding planes. The grey coloured silt and clay sediments produced the majority of the *Puijila* fossil material.

The climate in that area of the Arctic, at the time of the deposition of the Haughton Formation, was different than what is currently experienced in the crater (Hickey et al., 1988; Whitlock and Dawson, 1990; Osinski and Lee, 2005).

Palynomorph analysis of sediments from the crater by Hickey et al. (1988) produced a picture of a cool-temperate climatic regime. Whitlock and Dawson's (1990) comparisons of fossil pollen from the crater to modern assemblages inferred the climate to be humid, with severe winters and a maritime coastal effect. Both studies found palynological evidence for the presence of a mixed conifer and hardwood forest, with a mean average

temperature estimated at 8°C to 12°C and a growing season of 120 to 200 days (Hickey et al., 1988; Whitlock and Dawson, 1990). During the early Miocene the crater would have experienced the same photo-periodicity that it does in modern times (Whitlock and Dawson, 1990).

The fossil vertebrate assemblage is consistent with a cool temperate habitat. In particular, fossil remains of smelt and trout suggest a cool water environment. The fossil remains of rabbit, shrew, rhinoceros, deer and swan also indicate the environmental conditions in the crater was less severe than it is today (Hickey et al., 1988; Whitlock and Dawson, 1990). The fossil fauna discovered in the crater lake sediments display a high level of endemism (Hickey et al., 1988). *Puijila* is currently the only carnivore to have been discovered in the Haughton Formation (Hickey et al., 1988; Whitlock and Dawson, 1990; Rybczynski et al., 2009).

CHAPTER 1 - THE PECTORAL GIRDLE AND FORELIMB OF *PUJILA DARWINI*

INTRODUCTION

Pinnipedia is an aquatically specialized group of marine mammals that includes Phocidae (seals), Otariidae (sea lions) and Odobenidae (walrus). The group is now widely considered to be monophyletic and Musteloidea is considered the most likely sister taxon (Flynn et al., 2005; Fulton and Strobeck, 2006; Sato et al., 2006; Finarelli, 2008). Before these relatively recent molecular phylogenetic studies, it had been hypothesized, based on morphological and paleontological evidence, that pinnipeds were biphyletic. Otariids were hypothesized to be closely related to ursids (bears) and phocids were thought to have a sister-group relationship with mustelids (weasles) (Tedford, 1976) (Fig. 2).

FIGURE 2. Simplified phylogenies depicting the various hypothesized relationships of the of the modern pinnipeds families; **A**, the biphyletic hypothesis; **B**, the more recent monophyletic hypothesis. The names of the modern pinnipeds families are in **bold**.

Modern pinnipeds also have distinctly different swimming modes. Obobenids and phocids are primarily hindlimb dominated swimmers, and otariids are forelimb dominated swimmers (Howell, 1929; Tarasoff et al., 1972; Demere et al., 2003; Bebej, 2008). Although the idea that pinnipeds derived from separate terrestrial ancestors has

been widely replaced with the idea of a single origin based on both molecular and morphological evidence, there is little fossil evidence from the earliest stages of pinniped evolution. This creates gaps in our understanding of the ecology and morphology of the transitional ancestors of pinnipeds and how they could lead to the variety of swimming modes displayed by modern pinnipeds.

Despite their different swimming styles, pinnipeds share similarities in their forelimb osteology. The humeri of pinnipeds have enlarged greater and lesser tuberosities, a deep and rounded bicipital groove, large raised deltoid crests, large lateral epicondylar wings and a deep trochlea. The radii appear “club-like” because they expand anteriorly in the distal half and have a large rounded radial head. The ulna has an expanded and hook-like olecranon process and a shallow trochlear notch (Howell, 1929; English, 1977). The greatest difference between the osteology of phocids and otariids is seen in the scapulae. However, despite the differences in the general morphology of the element, they share a posterodorsal expansion for an enlarged teres musculature (Howell, 1929; English, 1976; Tedford, 1976). In order to better understand the early evolution of the pinniped lineage, and how two such different swimming modes could evolve, an improved understanding of the swimming behaviour of the earliest pinnipeds becomes essential.

Puijila darwini, described by Rybczynski et al. (2009), represents a morphological intermediate between extant pinnipeds and their terrestrial ancestors. The preliminary description of the holotype specimen of *Puijila* focused on cranial characters and a

phylogenetic analysis grouped it in a clade with *Potamotherium* and the stem pinniped *Enaliarctos*. Of these genera, the postcranial remains of *Puijila* appear the least aquatically specialized.

Although the initial description did not focus on the postcrania, Rybczynski et al. (2009) did make preliminary observations about *Puijila*'s musculoskeletal specializations for swimming and possible modes of locomotion. Superficially, *Puijila* appears otter-like and resembles *Lontra canadensis*. It differs by having a manus and pes which are proportionally larger, a shoulder region which is more specialized and overall, a more robust skeleton than *Lontra*. Its large feet and unspecialized tail led Rybczynski et al. to tentatively conclude that it swam by quadrupedal paddling. This is a form of locomotion which could have given rise to both the fore and hindlimb dominated swimming modes displayed by modern pinnipeds (Fish, 1996).

The holotype specimen of *Puijila* (NUFV-405) was ~65% complete when it was first described, and more fragments have since been collected from the same individual. This provides a unique opportunity to study the musculoskeletal swimming specialization of a stem pinniped in more depth. Here I present the first comparative description of the forelimb of *Puijila darwini*, and attempt to assess its possible modes of swimming, with the aim of providing some insights into the earliest stages of pinniped evolution.

MATERIAL AND METHODS

The holotype material examined for *Puijila darwini* (NUFV-405) is housed at the Canadian Museum of Nature (CMN) in Ottawa, Ontario and represents ~80% of a single, male individual. The specimen is curated as part of the Nunavut Fossil Vertebrate Collection. The skeletal elements of the forelimb and pectoral girdle were examined for the purpose of this study and included the left and right partial scapulae, complete right and partial left humerus, complete left and right radii and ulnae, the right triquetrum and hamate, both scapholunars and pisiforms, right metacarpals I, II, IV, V and left metacarpals II-V and multiple examples of proximal, intermediate and ungual phalanges. The primary comparative materials used in the description were specimens of the semi-aquatic musteloid *Lontra canadensis* (river otter - CMNMA-Z170, USNM-256976), various specimens of the fossil *Potamotherium vallentoni* (Table 1) and terrestrial musteloids specimens *Mephitis mephitis* (striped skunk - CMNMA-4828, CMNMA-75568) and *Martes americana* (american marten - CMNMA-11785). Other specimens examined for the description included of the semi-aquatic musteloids *Enhydra lutris* (sea otter - CMNMA-6283) and *Pteronura braziliensis* (giant otter - USNM-304663); the terrestrial musteloids *Gulo gulo* (wolverine - CMNMA-4389), *Procyon lotor* (raccoon - CMNMA-41037) and *Martes pennanti* (fisher - CMNMA-3894); the extant pinnipeds *Halichoerus grypus* (grey seal - CMNMA-52829) and *Eumetopias jubatus* (northern sea lion - CMNMA-2609) and the fossil pinniped *Enaliarctos mealsi* (USNM-250345).

TABLE 1. Specimens of *Potamotherium vallentoni* examined for the comparative description.

Scapula	NMB-Ma.704, NMB-Ph.1368, NMB-Ph.3661, NMB-Sg.361, NMB-Sg.369, NMB-Sg.3188, NMB-Sg.4367, NMB-Sg.4369, NMB-Sg.4375, NMB-Sg.5579, NMB-Sg.6970, NMB-Sg.6991, NMB-Sg.7622, NMB-Sg.7623, NMB-Sg.7624, NMB-Sg.7626, NMB-Sg.17975, NMB-Sg.18133, NMB-Sg.18552, NMB-Sg.19899, NMB-Sg.21224, NMB-Sg.21225, NMB-Sg.21226, NMB-Sg.21227, NMB-Sg.21228, NMB-Sg.21231, NMB-Sg.21232
Humerus	NMB-Sg.7627, NMB-Ph.3665, CMNFV-54090
Radius	NMB-Ma.2827, NMB-Ma.2838, NMB-Ma.2839, NMB-Sg.10830, NMB-Sg.3195m, CMNFV-54093, CMNFV-54093
Ulna	NMB-Ma.2830, NMB-Sg.7629, NMB-Sg.7634, NMB-Sg.7639, NMB-Sg.11346, NMB-Sg.22328, CMNFV-54091, CMNFV-54092
Carpals	<i>Scapholunar</i> - NMB-Sg.097, NMB-Sg.17653; <i>Pisiforme</i> - NMB-Sg.6351; <i>Triquetrum</i> - NMB-Sg.11368, NMB-Sg.ii368; <i>Hamate</i> - NMB-Sg.373i
Metacarpal I	NMB-Ma.2894, NMB-Ma.2896, NMB-Sg.i298, NMB-Sg.i628i, NMB-Sg.1734, NMB-Sg.14073
" II	NMB-Ma.976, NMB-Sg.i396i, NMB-Sg.3524, NMB-Sg.13565
" III	NMB-Sg.4438, NMB-Sg.7002, NMB-Sg.13569, NMB-Sg.2i307, NMB-Sg.2i3i3
" IV	NMB-Sg.1738, NMB-Sg.7036, NMB-Sg.16024, NMB-Sg.18576, NMB-Sg.2i3i2, NMB-Sg.23060
" V	NMB-Sg.ii309, NMB-Sg.ii3i2, NMB-Sg.8036, NMB-Sg.10891, NMB-Sg.19724, NMB-Sg.2009i
Phalanges	<i>Proximal</i> - NMB-Sg.3923, NMB-Sg.i3975, NMB-Sg.i4208, CMNFV-54100, CMNFV-54101, CMNFV-54102, CMNFV-54103; <i>Intermediate</i> - NMB-Sg.i4090, NMB-Sg.i42i3, NMB-Sg.17650, CMNFV-54104
Unguals	NMB-Sg.ii404, NMB-Sg.9581

Literature comparisons also referred to include: Evans (1993) (terrestrial Carnivora); Savage (1957) (*Potamotherium valletoni*); Howell (1929), English (1976, 1977), Berta and Ray (1990), Berta and Wyss (1994), Berta (1994) (modern and fossil Pinnipedia); Howard (1973), Fischer (1942) (Lutrinae); Hall (1926, 1927); Leach (1977b, a) (terrestrial Musteloidea).

Institutional abbreviations—**CMN**, Canadian Museum of Nature, Ottawa, Canada;

USNM, National Museum of Natural History, Washington, District of Columbia; **NMB**,

Naturhistorisches Museum Basel, Basel, Switzerland.

MORPHOLOGICAL DESCRIPTION OF THE FORELIMB

Scapula

There are two partial scapulae that together represent the majority of the scapula with the exception of its anterior portion. Both glenoids, both caudal borders, the majority of the left dorsal border and the left and right scapular spines are preserved as articulated fragments (Fig. 3). Only a little of the supraspinatus fossa is preserved. The scapula of *Puijila* does not resemble terrestrial musteloids and shows only a slight resemblance to *Lontra*. It has the greatest similarity to that of *Potamotherium*, though it is less specialized.

The scapula of *Puijila* shares with *Lontra* a narrow infrapinatus fossa which is reduced relative to the supraspinatus fossa, a raised scapular spine and a caudal border with an enlarged infraglenoid tubercle. Compared to the humerus, the scapula of *Puijila* is proportionally larger than that of *Lontra* and *Potamotherium*. From the glenoid cavity to dorsal margin, it extends nearly 84% the length of the humerus, compared with 75% in *Potamotherium* and 78% in *Lontra*, according to the measurements of Savage (1957). The scapula of *Puijila* also differs from *Lontra* by possessing a more robust scapular spine and caudal border, a robust and raised dorsal border, a deeper and narrower infrapinatus fossa and a proportionally larger triceps muscle scar, characteristics which are shared by *Potamotherium*. The greatest similarity between *Puijila* and *Potamotherium* is an area of posterodorsal expansion of the scapula, presumably for the teres major muscle, separated from the infrapinatus fossa by a small ridge - called a

FIGURE 3. Scapulae of *Puijila darwini*, NUFV-405. A, left scapula, lateral view; B, right scapula, lateral view; C, glenoid, left scapula, anteroventral view; D, reconstruction of the scapula of *Potamotherium vellentoni* (updated from Savage, 1957 using specimens from the Naturhistorisches Museum Basel listed in Table 1.) This reconstruction of the scapula is used for the comparative description of *Puijila*. Abbreviations: CA, caudal angle; CB, caudal border; CP, coracoid process; DB, dorsal border; G, glenoid; IF, infraspinatus fossa; IT, infraglenoid tubercle; M, metacromion; S, scapular spine; S¹, secondary spine; SF, supraspinatus fossa; TF, teres fossa; b, origin of biceps muscle; d, origin of deltoid muscle; is, origin of infraspinatus muscle; ss, origin of supraspinatus muscle; t₁, origin of triceps musculature (long head); te¹, origin of teres major muscle. Scale bars equal 1cm.

“secondary spine” by Savage (1957). Compared to *Lontra*, *Puijila* and *Potamotherium* also possess a smaller scapular notch, slightly rounder glenoid, a larger supraglenoid tubercle, larger medially extended coracoid process and a more robust and proportionally shorter scapular spine. The acromion and metacromion of *Puijila* is only partially preserved, but appears similar to *Potamotherium*, having indications of a large metacromion and lacking the distinct indentation between the two processes, as seen in *Lontra*. *Puijila* differs from *Potamotherium* in having a proportionally smaller area of postero-dorsal expansion and a less distinct secondary spine, a shallower scapular notch, proportionally smaller triceps scar, a proportionally less robust scapular spine, less narrowing of the infraspinatus fossa and a proportionally larger scapula overall.

Humerus

The humerus of *Puijila* is represented by a complete right and partial left humerus (Fig. 4). The partial left humerus preserves the shaft with incomplete proximal and distal epiphyses. The humerus of *Puijila* resembles lutrines rather than terrestrial musteloids, and also shows some characteristics in common with *Potamotherium*.

The humerus of *Puijila* differs from terrestrial musteloids, such as *Mephitis* and *Martes*, by having a robust, anteriorly curving shaft, a prominent and enlarged deltopectoral crest, enlarged greater and lesser tuberosities, medial epicondyle and lateral epicondylar wing. These characteristics, in addition to being reduced in length relative to the ulna, give it a superficial resemblance to that of *Lontra*. However, there is

FIGURE 4. Right humerus of *Puijila darwini*, NUFV-405. A, lateral view; B, anterior view; C, medial view; D, posterior view; E-H, images from 3D surface scan data. Abbreviations: BG, bicipital groove; CA, capitulum; DC, deltopectoral crest; GT, greater tuberosity; H, humeral head; LE, lateral epicondyle; LEW, lateral epicondylar wing; LT, lesser tuberosity; ME, medial epicondyle; MEF, medial epicondylar foramen; OF, olecranon fossa; T, trochlea; a_l , insertion of lateral anconeus muscle; a_m , insertion of lateral anconeus muscles; br, origin of brachialis muscle; d, insertion of deltoid muscle; e, origin of extensor muscles; f, origin of flexor muscles; is, insertion of infraspinatus muscle; p, insertion of pectoralis muscle; pt, origin of pronator teres muscle; su, origin of supinator muscle; ss, insertion of supraspinatus muscle; t, origin of triceps musculature; te^1 , insertion of teres major muscle; te^2 , insertion of teres minor muscle. Scale bars equal 1cm.

a greater expansion of the greater and lesser tuberosities, creating a deeper bicipital groove, when compared to that of *Lontra*. *Puijila* possesses a more robust and distinct lateral epicondylar ridge, than that of *Lontra*, which is located on the margin of the lateral epicondylar wing. The medial epicondyle is slightly more enlarged and expands further ventrally in *Puijila* and the trochlea of its humerus is deeper and steeper sided. The most striking difference between the humerus of *Lontra* and *Puijila* is the greater expansion of the deltopectoral crest in the latter. The crest extends two thirds the length of the shaft in *Puijila* and only half the length of the shaft in *Lontra*. The deep bicipital groove, robust medial epicondyle and lateral epicondylar ridge, deep and steeply sided trochlea and long deltopectoral crest of *Puijila*, all resemble those of *Potamotherium*. *Potamotherium* and *Puijila* show a similar degree of enlargement in the tuberosities of the humerus and both possess a larger medial epicondylar foramen than those of *Lontra* or *Martes*. However, *Puijila* differs from *Potamotherium* by possessing a proportionally smaller lateral epicondylar wing, having lesser ventral expansion of the medial epicondyle and a slightly shallower trochlea. The deltopectoral crest of *Puijila* is enlarged, but is unlike the anteriorly expanded and raised high ridge of bone seen on the humeri of pinnipeds and *Potamotherium*; which is referred to as the “deltoid crest” in modern pinnipeds (Howard, 1929; English, 1977).

Radius

Both radii are fully represented in the holotype specimen of *Puijila darwini*, though the left is severely weathered (Fig. 5). The radius of *Puijila* appears similar to

FIGURE 5. Left radius of *Puijila darwini*, NUFV-405. A, medial view; B, anterior view; C, lateral view; D-F, images rendered from 3D surface scan data of the same radius. Abbreviations: AC, articular circumference; AF, articular fovea; BT, biceps tubercle; H, radial head; N, radial neck; SP, styloid process of the radius; gedcd, groove for the tendon of the extensor carpi digitorum muscle; gecr, groove for the tendon of the extensor carpi radialis muscle; gedl, groove for the tendon of the extensor digitorum lateralis muscle; gepb, groove for the tendon of the extensor pollicis brevis muscle; im, attachment of interosseous membrane; pb, origin of extensor pollicis brevis muscle; pq - insertion of pronator quadratus muscle; pt, insertion of pronator teres muscle; su, insertion of supinator muscle. Scale bars equal 1cm.

both Lutrinae and *Potamotherium*, by being more robust and more convex anteriorly than the radii of terrestrial musteloids such as *Martes* and being flattened mediolaterally and expanded antero-posteriorly the distal half. *Puijila* also shares with *Lontra* and *Potamotherium* an enlarged radial head, large biceps tubercle, a deep bicipital pit and a mediolaterally flare on the distal end of the radius. In *Puijila*, the mediolateral expansion of the distal radial epiphysis occurs to a similar degree as in *Lontra*. The bicipital pit, located on the proximal side of the biceps tubercle of the radius is larger than in *Lontra*, but not as deep as that of *Potamotherium*. The radial shafts of *Puijila* and *Potamotherium* lack the ridge of bone, for the attachment of the interosseous membrane, as seen in *Lontra*, and instead display an oval tubercle for its attachment in a similar position on the bone. The styloid process is expanded and more pointed in *Puijila* than in *Lontra*, and the ulnar articulation is smaller and oriented more ventrally. Compared to *Lontra*, *Puijila* displays deeper grooves for the tendons of the extensor carpi radialis, extensor communis digitorum and extensor metacarpi muscles; causing the styloid process to appear elevated. *Puijila* and *Potamotherium* have a unique triangular tubercle on the medial side of the distal end of the radius, which is absent in *Lontra*. The anterior side of that tubercle forms part of the extensor metacarpi groove. *Puijila* further differs from *Lontra*, *Potamotherium* and the terrestrial condition by having a more circular articular fovea, a thick articular circumference that extends around two thirds of the radial head, and being generally more robust. These characteristics combined make the overall shape of the head somewhat similar to modern pinnipeds.

Ulna

The holotype specimen of *Puijila* includes left and right ulnae, both of which are well preserved (Fig. 6). The ulna of *Puijila* is similar to that of the larger specimens of *Potamotherium*. It is more gracile than that of *Lontra* and smaller specimens of *Potamotherium*, and slightly resembles that of *Mephitis*. Unlike terrestrial musteloids, *Puijila* possesses an olecranon which is proportionally larger and more robust than that of terrestrial musteloids and *Lontra*, yet less expanded than that of *Potamotherium*. On the olecranon, there are large areas of attachment for the triceps musculature on the proximal surface and along the posterior portion its lateral side. The ulna of *Puijila* can be distinguished from *Potamotherium* by a large lateral tuberosity on the olecranon that covers the ventral half of the lateral face of the olecranon and tapers to a point distally. Like *Potamotherium*, the olecranon of *Puijila* is narrowest at its center and has a pronounced expansion toward its proximal end and anconeal process. This gives it an hour-glass outline in anterior view. It appears to project medially, as compared to that of *Lontra*, and this is driven by the medial and ventral expansion of the posterior margin of the olecranon. The trochlear notch of *Puijila* and *Potamotherium* is more open than in *Lontra*, whose notch is more convex and whose anconeal and coronoid processes draw closer together with ontogenic age (Fischer, 1942). However, the trochlear notch of *Puijila* is less open than that of *Potamotherium* or flippered pinnipeds. The radial notch of *Puijila* is similar in shape to that of *Potamotherium*, being larger, more circular

and inclined further from the antero-posterior axis of the ulna, than that of *Lontra*.

There is a deep groove for the brachialis muscle just distal to the trochlear notch. The shaft of the ulna narrows distally and is roughly triangular in cross section. The posterior margin of the shaft, distal to the trochlear notch, has a gentle curvature that makes it dorsally convex. This is strikingly different from the robust, straight and stout ulna of *Lontra*. There is a prominent tubercle on the lateral portion of the midpoint of the shaft for the attachment of the interosseous membrane, which is proportionally larger and more robust in *Puijila* than the condition seen in *Potamotherium* and *Lontra*. In both *Potamotherium* and *Puijila*, this interosseous tubercle is expanded laterally and gives the ulnar shaft a bent appearance. The distal portion of the ulnar shaft is expanded mediolaterally as compared with that of *Lontra* and *Potamotherium* and the styloid process is proportionately smaller in *Puijila* than in *Lontra*, though similarly shaped in lateral view. The pisiform facet on the styloid is half-moon shaped in *Puijila*, resembling that of *Potamotherium*, but u-shaped in *Lontra*. The surface itself is angled more anteriorly than that of *Lontra*, in both *Puijila* and *Potamotherium*.

Carpals

The carpal bones preserved in *Puijila* are the left and right scapholunars and pisiforms and the right triquetrum and hamatum (Fig. 7). The general arrangement of the carpals is the same as the terrestrial musteloid condition, though the shape of each bone differs slightly. The shapes of the carpals of *Puijila* are most similar to *Potamotherium* and together they resemble *Lontra* (Fig. 7). As Savage (1957) observed,

FIGURE 7. A, Diagram showing the proposed arrangement and articulations of the left carpals of *Potamotherium vallentoni*, (modified from Savage, 1957); B, proposed arrangement and articulations of the left carpals of *Puijila darwini* (*indicates bones not preserved in NUFV-405; dotted lines represent assumed articulations between the missing elements); C, right scapholunar, in dorsal and ventral views; D, right triquetrum, in medial and dorsolateral view; E, right hamatum, in medial, dorsal and lateral view; F, right pisiform, lateral, dorsal and ventral views; G-J, images of the same elements rendered from 3D surface scanning data. Abbreviations: C, capitulum; H, hamatum; P, pisiform; R, radius; S-L, scapholunar; T, trapezium; Td, trapezoid; Tq, triquetrum; UI, ulna; I-V, metacarpals I to V; X^f, facet, of element "X". All scale bars equal 1cm.

Potamotherium has carpals which were similar to those of *Lontra* and that show none of the specializations of those of pinnipeds.

Pisiform—The pisiform of *Puijila* displays similarities with *Potamotherium* and *Lontra*, but also resembles the condition of the terrestrial musteloids *Martes* and *Mephitis*. The shape of the ulnar and triquetrum facets in *Puijila* resembles those of *Potamotherium*, being larger and more rounded than those of *Lontra* and *Martes*. These facets meet, forming a triangular cross-section in lateral view. *Puijila* differs from *Potamotherium* in that the junction of the two facets curves inward, not outward, in dorsal view, an appearance also shared by *Lontra* and *Martes*. *Puijila* also differs from *Potamotherium* in that it lacks the anteroposterior expansion of its posterior end, which gives the pisiform of *Potamotherium* an hourglass outline in both dorsoventral and mediolateral aspect. The ventral portion of the pisiform of *Puijila* is less reduced than that of *Lontra*, resembling *Martes*, *Mephitis* and *Potmotherium*. *Puijila* differs from *Martes* and *Mephitis* by having a more robust pisiform that displays a greater dorsoventral expansion at its ventral end.

Scapholunar—The scapholunar of *Puijila* appears more similar to *Potamotherium* than to *Lontra* and terrestrial musteloids, such as *Martes*. A difference between the scapholunars of *Puijila* and *Martes* is the shape of the trapezium and trapezoid facets. Those of *Puijila* are more distinct from one another and the trapezium facet of *Puijila* is deeper than that of *Martes*. *Puijila* also has a proportionally wider scapholunar medilaterally and enlargement and increased robusticity of the sesamoid process, as

compared with *Martes*. The sesamoid process of *Puijila* is also proportionally more enlarged than *Lontra*, and has a similar level of expansion to that of *Potamotherium*. Compared to *Lontra*, *Puijila* has a less rectangular radial facet and a smaller angle, and greater distinction, between the trapezium and trapezoid facets. The scapholunar of *Puijila* appears most similar to *Potamotherium* and both appear more heart shaped in dorsal view, unlike the rectangular outline of those of *Martes* and *Lontra*. *Puijila* differs from *Potamotherium* by having more ovoid and anteroposteriorly compressed capitatum and hamatum facets, a proportionally smaller trapezium facet, which is more ovoid than circular, and a radial facet which is slightly more elongate mediolaterally.

Triquetrum—The triquetrum of *Puijila* is has a shape which is reminiscent of terrestrial musteloids such as *Martes*, but is lengthened anteroposteriorly like *Lontra* and *Potamotherium*, giving it an almost rectangular outline in lateral and medial view. Its dorsolateral surface appears most similar to that of *Lontra*, but its medial surface is more similar to that of *Potamotherium*. The positioning and orientation of the ulnar and pisiform facets, on the dorsolateral side of the triquetrum of *Puijila* generally resembles those of *Lontra* and *Martes*, but the ulnar facet of *Puijila* and *Lontra* is deeper than that of *Martes*. The ulnar facet of *Puijila* is proportionally smaller than the pisiform facet, whereas in *Lontra* they are roughly equal size. The medial side of the triquetrum of *Puijila* also differs from *Lontra*, whose large hamatum facet is similar in shape to terrestrial musteloids. *Puijila* has a proportionally smaller hamatum facet and a more distinct, larger metacarpal V facet than *Lontra* or terrestrial musteloids. The shape and

relative proportion of these facets in *Puijila* are closer to those of *Potamotherium*.

Puijila differs from *Potamotherium* by having a proportionately smaller metacarpal V facet and larger hamatum facet and proportionately smaller pisiform facet and larger ulnar facet.

Hamatum—The shape of the hamatum of *Puijila* is similar to that of *Potamotherium* and *Lontra*, but differs from terrestrial musteloids, such as *Martes*. Unlike *Martes*, the dorsal surface of the hamatum of *Puijila* is expanded anteriorly to form a triangular wedge, which points between metacarpals IV and V. The hamatum of *Puijila* is similar to that of *Lontra*, but the metacarpal IV and V facets are more distinct from one another, and the articulation surface they create is more concave, in *Puijila*. The hamatum of *Puijila* and *Potamotherium* have similar shaped triquetrum and capitulum facets, which are more rectangular than those of *Lontra*.

Manus

The right metacarpals I, II, IV and V and the left metacarpals II, III, IV and V of *Puijila* were recovered. All the metacarpals present are in good condition with little weathering and no breakage. The metacarpals do not immediately resemble those of terrestrial musteloids, being more robust than *Martes*, more elongate than *Mephitis* and possessing more robust epiphyses than either (Fig. 8). They are proportionately longer than those of *Lontra* and are more similar in size and shape to the modern lutrine, *Pteronura*. The metacarpals of *Puijila* broadly resemble those of *Potamotherium*, but differ by being proportionately shorter, more robust proximally and slightly more gracile

FIGURE 8. Reconstruction of the left manus of *Puijila darwini*, NUFV-405 rendered from 3D imaging data. A, dorsal view; B, ventral view. Abbreviations: I-V, manual digits I to V; Mc, metacarpal; Phⁱ, intermediate phalanx; Ph^p, proximal phalanx; Un, ungual phalanx. All scale bars equal to 1 cm.

distally. The shape of the manus of *Puijila* differs from *Potamotherium*, as metacarpals I and V are shorter in comparison to II, III, and IV, resembling the proportions of those of *Lontra*. However, the entire manus of *Puijila* is proportionally much larger than that of *Lontra* and metacarpal II is noticeably longer than metacarpal V, a condition shared by *Potamotherium*. The order of the length of the metacarpals in *Puijila* is $3 \geq 4 > 2 > 5 > 1$, as compared to $4 \geq 3 > 2 \geq 5 > 1$ in *Lontra* and $4 \geq 3 > 2 > 5 > 1$ in *Potamotherium*.

The phalanges of *Puijila* are well represented, with at least one of proximal phalanges I-V, intermediate phalanges III-V and ungual phalanges III-V, being represented by either a right or left element. They appear almost identical to those of *Potamotherium*, also being similar to *Lontra* and differing from terrestrial musteloids, by being flattened dorsoventrally and elongated relative to their associated metacarpal. The greatest degree of dorsoventral flattening occurs in the proximal phalanges of *Puijila* and is not uniform between the proximal and intermediate phalanges like in *Lontra*.

Metacarpal I—Metacarpal I differs from *Potamotherium* by having a shaft which is more flared proximally. The metacarpal is unlike *Potamotherium* as it is concave in lateral view. It resembles *Pteronura*, in that respect, though the curvature in *Puijila* is slightly more pronounced. The proximal end of the bone expands further ventrally in *Puijila* than in *Potamotherium*. The metacarpal I of *Puijila* has a deeper elongate u-shaped trapezium facet than that of *Lontra*, which has a shallower and more triangular facet.

Metacarpal II—In *Puijila*, metacarpal II differs by being less robust than that of *Potamotherium*. The shaft of the bone is more slender and lacks a tuberosity which appears prominently on the proximal half of the medial surface of that of *Potamotherium*. The metacarpal appears similar to *Potamotherium* in all other respects. It is also similar to that of *Lontra*, except for being proportionately longer.

Metacarpal III—The metacarpal III, of *Puijila*, appears similar to *Potamotherium* and *Lontra*, but has a more slender shaft and a gentle tapering of its proximal end. Its lateral articulation surface extends only slightly over the adjacent metacarpal IV capitulum facet, causing the proximal end to appear to slant laterally in dorsal view, in addition to the narrowing. This is distinct from the square proximal epiphysis seen in *Potamotherium* and *Lontra*. Also, the articulation between metacarpal III and metacarpals II and IV appears better fitted than in *Potamotherium* and *Lontra*. The element is slightly more convex than that of *Potamotherium* and proportionally longer than in *Lontra*.

Metacarpal IV—*Puijila* differs from *Potamotherium* by having less mediolateral expansion at its proximal end and a tuberosity located ventrally on the lateral surface of the shaft, just distal of the lateral articulation for metacarpal V. The bone is expanded dorsally in the proximal half of the bone, as compared with *Potamotherium*. The bone has a similar curvature to that of *Potamotherium*. The proximal articulation surface narrows more, ventrally, in *Puijila*. The articular facets at the proximal end of the element, for metacarpals III and V, taper towards each other creating a v-shaped outline

in dorsal view in *Puijila*. This is unlike the metacarpal IV of *Lontra*, where the proximal end of the bone is shaped like a parallelogram in dorsal aspect. Metacarpal IV of *Puijila* is also proportionately longer than that of *Lontra*.

Metacarpal V—The metacarpal V, of *Puijila*, is distinct from that of *Potamotherium* as it curves medially and appears slightly more convex in lateral view. It is somewhat similar in appearance to that of *Lontra*, but is less dorsoventrally flattened and narrower mediolaterally in its proximal half. In most respects it appears almost identical to that of *Potamotherium*, including the shape and relative size of its proximal articulation surfaces.

Proximal Phalanges—The proximal phalanges of *Puijila* are elongated to approximately 70% the length of the metacarpals. They differ from those of terrestrial musteloids, such as *Martes* and *Mephitis*, by being dorsoventrally flattened. They differ from those of *Lontra* by having a slightly greater degree of flattening and elongation of the elements. *Puijila*, *Potamotherium* and *Lontra* possess a widening toward the distal portion of the shaft of the proximal phalanges, associated with two ventral tubercles located on the medial and lateral sides of the ventral shaft surface, just proximal to the distal articulation of the element. These are larger in *Puijila* than in *Lontra*, and associated with a greater degree of mediolateral expansion in that area of the element. The phalangeal shafts of both *Puijila* and *Potamotherium* appear slightly more slender, elongate and gracile than those of *Lontra*. The epiphyses of the phalanges of *Puijila* show the same trend of enlargement and robusticity as seen in the metacarpals.

Intermediate phalanges—The intermediate phalanges of *Puijila* resemble those of *Potamotherium*, but differ slightly by possessing a lesser degree of elongation, anteroposterior flattening and mediolateral expansion. They differ from those of *Lontra* by being less flattened and more gracile. Also, the proximal articular surfaces of the intermediate phalanges of *Puijila* and *Potamotherium* are different from those of *Lontra*. In *Puijila* and *Potamotherium*, they are shallower and crossed by a dorsoventrally aligned ridge, which separates the medial and lateral side of the articular surface into two oval pits. In dorsal view, there is a small lip of bone jutting out into the center of the articular surface, which is the dorsal termination of the ridge. The entire shape of the articular surface gives the proximal end of the intermediate phalanges, of both *Puijila* and *Potamotherium*, a shallow w-shaped outline in dorsal view, as opposed to the simple u-shaped outline of that of *Lontra*. The articular surface in terrestrial musteloids, such as *Mephitis* and *Martes*, appears similar in shape to that of *Puijila* and *Potamotherium*, but are slightly deeper. The rest of the element is not similar to *Puijila* and *Potamotherium*, as it is not flattened in the terrestrial forms. Therefore, the intermediate phalanges of *Puijila* are less flattened than those of *Lontra*, being similar to those of *Potamotherium*, and possess a proximal articulation surface that is similar to terrestrial musteloids.

Ungual phalanges—The ungual phalanges are difficult to assign to a specific digit. Those included in this study have been tentatively assigned to digits III to V, based on their size and the shape of their articular surfaces. The other unguals found in association with the *Puijila* skeleton have been tentatively associated with the pes. The

ungual phalanges of *Puijila* appear similar to those of *Lontra* and *Potamotherium*, being slightly reduced in size and rounded at their tips, relative to some terrestrial musteloids such as *Mephitis*. They appear less reduced than those of *Potamotherium* and similar to those of *Lontra*. They are greatly reduced in size and length when compared to a digging specialized musteloid, such as *Taxidea taxus*.

TABLE 2. Measurements (in mm) of the forelimb skeleton of *Puijila darwini*.

Measurement	Right	Left
Scapula, length(glenoid cavity to dorsal border)	77.82*	81.05*
Scapular spine, max. height	NA	13.86*
Teres expansion, max length	NA	33.04*
Teres expansion, max width	13.87*	15.53*
Humerus, max. length	97.22	95.12*
Deltopectoral crest, length	56.89	NA
Distal condylar, width, ml	29.82	NA
Diaphysis, diameter, ml	8.37	8.18
Diaphysis, diameter, ap	15.06	15.28
Radius, max. length	73.77	73.39
Diaphysis, diameter, ml	7.23	7.01
Diaphysis, diameter, ap	7.82	7.43
Ulna, max. length	97.48	96.8
Functional length (styloid to coronoid process)	66.62	66.81
Olecranon, max. length	15.87	17.43
Diaphysis, diameter, ml (of func. length)	6.03	5.88
Diaphysis, diameter, ap (of func. length)	7.54	7.93
Metacarpal I, max. length	23.22	NA
" II, max. length	30.58	30.81
" III, max. length	NA	36.46
" IV, max. length	35.93	35.76
" V, max. length	28.09	28.02
Proximal Phalanx I, max. length	21.95	NA
" II, max. length	23.92	23.5
" III, max. length	26.75	26.99
" IV, max. length	24.94	24.86
" V, max. length	22.78	22.84
Intermediate Phalanx III, max. length	18.06	18.4
" IV, max. length	17.34	17.4
" V, max. length	16.24	16.18
Ungual Phalanx III**, length	12.51*	11.73*
" IV**, length	11.89*	11.49*
" V**, length	10.85*	NA

*- measurements are affected by the element being fragmented.

** - digit association uncertain.

Abbreviations: ml, mediolateral; ap, anteroposterior.

DISCUSSION

The exceptional preservation of the forelimb of *Puijila darwini* allows for identification of specializations that may be shared with other members of the pinniped lineage and specializations that have functional implications and may be useful for behavioural reconstruction. Skeletal specializations of the forelimb of *Puijila* which are shared with *Potamotherium* and pinnipeds include the presence of a “teres fossa” on the scapula, a deep humeral trochlea, an enlarged greater and lesser tuberosity of the humerus, a proportionately large manus, a shallow trochlear notch of the ulna and a robust, rounded radial head. Other traits which could suggest a pinniped affinity are the robust deltopectoral crest of the humerus and an expanded olecranon. These skeletal features are more developed than in modern lutrines, but do not yet approach the condition seen in flippered pinnipeds and *Potamotherium*.

The specializations of the scapula in *Puijila* and *Potamotherium* indicate that many of their shoulder muscles were relatively larger than those of modern musteloids, including the semi-aquatic *Lontra* (Savage, 1957), but less robust than those of flippered pinnipeds. The specializations of the scapula which indicate enlargement or strengthening of muscle groups in *Puijila* include: a large infraglenoid tubercle, for the origin of the long head of the triceps, and an enlarged coracoid process, presumably for the origin of the biceps and coracobrachialis (Savage, 1957; Howard, 1973; Evans, 1993).

The coracobrachialis muscle, which sometimes originates from the coracoid process, is absent in *Lontra* and modern pinnipeds (Howell, 1929; Fischer, 1942). It is

also absent in some terrestrial musteloids, such as *Mephitis*, *Spilogale* and *Taxidea*, seeming to only exist in *Martes* (Hall, 1926, 1927; Leach, 1977b). In *Martes*, the coracobrachialis and biceps muscles both originate from the coracoid process, but in *Lontra*, modern pinnipeds and the other terrestrial musteloids the coracoid process is the site of the origin of the biceps muscle only (Hall, 1926, 1927; Howell, 1929; Fischer, 1942; Savage, 1957; Leach, 1977b). If *Puijila* did not possess a coracobrachialis, then only the enlarged biceps muscle would originate on the coracoid process of the scapula. Typically, the biceps muscle originates as a tendon which passes through the bicipital groove, between the greater and lesser tuberosities of the humerus. The main portion of the muscle is located along the anterior surface of the humerus, before again becoming a tendon which inserts onto the biceps tubercle of the radius. The main action of this muscle is as a forearm flexor (Fischer, 1942; Howard, 1973; Evans, 1993). In modern pinnipeds the coracoid process, from which the biceps muscle originates, is greatly reduced, but in the early fossil pinnipeds *Enaliarctos* and *Pteronarctos* it is larger and hook-like (Howell, 1929; Berta and Ray, 1990; Berta, 1994; Berta and Wyss, 1994). *Puijila* possess a coracoid process which is not reduced, being slightly enlarged in comparison to both *Potamotherium* and *Lontra*; possibly indicating a larger biceps muscle or an enlarged biceps and coracobrachialis muscle (Savage, 1957).

The infraglenoid tubercle, of both *Puijila* and *Potamotherium* is larger than those of terrestrial musteloids and *Lontra*, but its shape and position are similar. This would provide an enlarged area for the origin of the long head of the triceps; which, combined

with the other muscles of the triceps muscle complex, inserts onto the olecranon and acts to extend the elbow (Howard, 1973; Evans, 1993). The origin of the long head of the triceps in the sea lion *Zalophus* is also on the infraglenoid tubercle; similar to *Puijila*, *Potamotherium* and modern musteloids (Howell, 1929; Fischer, 1942; Howard, 1973; English, 1977; Evans, 1993). However, in the true seal *Phoca*, the position of the origin of the long head of the triceps is different; it originates from the posterodorsal edge of the infraspinatus fossa and along the dorsal margin of the scapula (Howell, 1929; English, 1977). The shape and size of the infraglenoid tubercle in *Puijila*, the likely origin for the long head of the triceps, suggests *Puijila* had a more robust musculature in the lower portion of the scapula, which was arranged similarly to modern musteloids. The lower portion of the scapula of *Puijila* shows great similarities to that of *Potamotherium*, indicating they likely possessed a similar arrangement of muscles; one that was less specialized, but similar in arrangement to what is found in some modern pinnipeds, such as *Zalophus*.

The most striking feature of the scapula of *Puijila* is the posterodorsal expansion, which can be interpreted confidently as providing attachment for an expanded teres major muscle. The teres major muscle originates from the lateral surface of the caudal angle in terrestrial and semi-aquatic musteloids and inserts on the medial side of the humerus, just below the lesser tuberosity (Fischer, 1942; Howard, 1973; English, 1977; Leach, 1977b, a; Evans, 1993). It provides adduction and flexion of the humerus (Evans, 1993). In pinnipeds the caudal angle is expanded forming a “teres fossa” that is

separated from the infraspinatus fossa by a ridge known as the “caudal scapular ridge” (English, 1977), or “secondary spine” (Savage, 1957) (Fig. 3). In *Lontra*, which can be considered one of the most swimming specialized of modern musteloids, there is no separated area of expansion on the scapula (Fischer, 1942). The expansion for the teres musculature in *Potamotherium* was noted by Savage (1957) to be comparable to the pinniped condition and similar areas of expansion appear in *Enaliarctos* and *Pteronarctos*. Therefore, this expansion may be associated with the pinniped condition, of the enlargement of the teres major muscle.

The deltoid muscle in terrestrial musteloids and *Lontra* is separated into the acromiodeltoid and spinodeltoid muscles which together originate from the scapular spine, metacromion and acromion and insert onto the deltoid ridge along the lateral side of the deltopectoral crest of the humerus (Hall, 1926, 1927; Fischer, 1942; Howard, 1973; English, 1977). The primary action of these two muscles is to abduct the humerus as well as contribute to its extension and external rotation (Fischer, 1942; Howard, 1973). In pinnipeds the deltoid is a single muscle, which in phocids originates on the acromion and along the length of the scapular spine, and in otariids continues further, turning to follow along the edge of the dorsal border, almost to the caudal angle (Howell, 1929; English, 1977). English (1977) performed gross dissections on 14 individuals of four species of otariids, including *Zalophus*, comparing them with terrestrial and semi-aquatic musteloids. He found that the expansion of the caudal angle in otariids was occupied with the teres major and the caudal fibers of the deltoid

muscle. English (1977) did not report a teres minor in *Zalophus*. However, Howell (1929), through observations of his dissections of two genera of modern pinnipeds, associated the area of expansion, or “teres fossa”, with the origin of the teres minor in *Zalophus* and the teres major in *Phoca*. Howell (1929) noted that the teres minor was distinct and located outside the infraspinus fossa between the infraspinus and teres major muscles, in both *Phoca* and *Zalophus*. This is unlike musteloids where the teres minor is often indistinguishable from the infraspinus and shares a close or common origin with the infraspinus when present (Hall, 1926, 1927; Fischer, 1942; Howard, 1973). The shape and position attributed to the origin of the caudal fibers of the deltoid in *Zalophus*, as described by English (1977), is the same as what Howell (1929) identified as the origin of the teres minor. In terrestrial mammals, the deltoid overlays the teres minor (Evans, 1993). Therefore, it is likely that these were two different names given to the same muscle. English (1977) suggested that the migration of the origin of the deltoid muscle allowed it to associate with the acromiotrapezius muscle and, by working together, these muscles would increase their functional length, thereby allowing for abduction of the forelimb through a greater range of movement, at a rapid rate and with a greater state of tension. Therefore, the presence of a posterodorsal expansion and secondary spine in *Puijila* indicates an enlargement of the teres major muscle and possibly also the teres minor muscle and may be associated with the enlargement, consolidation and migration of the deltoid muscle. It provides evidence that the muscles of the pectoral girdle of *Puijila* and *Potamotherium* may have resembled the condition of

the pinnipeds, rather than terrestrial or semi-aquatic musteloids.

The specializations of the humerus further support the indications of an enlarged biceps and deltoid musculature. The enlarged lesser and greater tuberosities of the humerus create a deep bicipital groove, which the biceps tendon pass through, and an enlarged deltopectoral crest, creating a larger area for the insertion of the deltoid and pectoralis muscles. The enlargement of the greater and lesser tuberosities of the humerus may also signify well developed supraspinatus and subscapularis muscles, and imply that the missing portion of the supraspinatus fossa was probably large in comparison to that of *Lontra*, possibly approaching the proportions seen in *Potamotherium* (Howell, 1929; Savage, 1957; English, 1977).

In *Puijila*, the relative size of the origin of the infraspinatus, as compared with the size of the suprascapularis, is smaller than in terrestrial musteloids. There is a deep groove for the infraspinatus insertion on the lateral facing side of the greater tuberosity of *Puijila*. Therefore, the infraspinatus appears to have still been a well developed muscle in *Puijila*. The area for the insertion of the teres minor is broken on both humeri, making it impossible to add to the partial evidence, provided by the scapula, that this muscle may have been separate from the infraspinatus in *Puijila*.

The expanded lateral epicondylar wing creates a large surface for attachment of the lateral anconeus muscle posteriorly and the brachialis muscle and extensor muscles of the wrist and hand anteriorly. Its proportionately larger size in *Puijila* and *Potamotherium* may indicate these muscles showed greater development in these two,

than in *Lontra*. Extensors that originate along the lateral margin of the lateral epicondylar wing include: extensor carpi radialis longus, extensor carpi radialis brevis, extensor digitorum communis and extensor digitorum lateralis (Howard, 1973; English, 1977; Evans, 1993). Together, these muscles dorsiflex the wrist and extend the digits away from the palm, while also stabilizing them in that position (Howard, 1973). Combining that motion with abduction of the digits would create a powerful opening and good stabilization of the manus; thus producing a large surface area that could be used for the creation of thrust in the water. The enlargements of the extensors in *Potamotherium* and *Puijila*, as compared to those of *Lontra*, were likely associated with the proportionately larger manus size. The medial epicondyle does not appear to have especially enlarged areas for the attachment of the corresponding flexors of the wrist and manus. However, there is well developed origin for the pronator teres muscle along its posterior margin.

Savage (1957) noted that the anterior curvature of the humeri of pinnipeds and *Potamotherium* made it similar to a bow, with tension being provided by the triceps musculature. According to Savage (1957), a curved humerus, such as that of *Puijila*, in conjunction with a strong triceps musculature, provides the strength to resist the strain caused by strong flexion and rotation of the forearm, without having to thicken the shaft.

The ulna and radius possess further indications of a powerful upper forelimb musculature, including an enlarged olecranon and area for the insertion of the triceps

musculature, a deep groove for the insertion of the brachialis, a large biceps tubercle of the radius and a large area for the insertion of the deep digital flexors and extensor indicis on the ulna.

The elements also display evidence that the forearm and hand musculature in *Puijila* were specialized. *Puijila* displays a robust insertion for the pronator quadratus muscle on both the radius and ulna. The large area of origin for this muscle and the mediolateral expansion of the distal ulna, are both indications for its enlargement in *Puijila*. It appears to have been more expanded in *Puijila* than in *Lontra*. There is a large area for the insertion of the supinator on the anterior side of the radius. The depth of the grooves for the tendons of the extensor muscles provides further evidence that *Puijila* had more specialized carpal and manus extensor musculature than *Lontra*, perhaps to support its proportionately larger manus.

The interosseus membrane serves as an attachment for muscles, stabilization of the radius and ulna and to translate movement of the radius to the humerus (English, 1976, 1977; Leach, 1977b, a; Evans, 1993). The robusticity of this structure in *Puijila* is indicated by the interosseus tubercles of the radius and ulna, which are both expanded. Savage (1957) observed that aquatic animals often hold the hand midway between pronation and supination during aquatic locomotion. English (1976, 1977) also observed that otariids hold the hand in this way and that they possess lower forelimb musculature that is designed to stabilize the radioulnar joint. He attributed this stabilization to the need to keep the forelimb flattened during aquatic locomotion, in order to increase

surface area during propulsion and to maintain a hydromechanical advantage while drawing the limb back through the water during the recovery stroke. Most of the rotary movement needed for the propulsive and recovery stroke of the forelimb during swimming is produced at the glenohumeral joint. Therefore, the main function of the pronator and supinator muscles is one of stabilization (English, 1976, 1977). This corresponds with the observations of Howell (1929) that pinnipeds had large pronator and supinator muscles, but due to the limited range of motion in their radioulnar joints, the muscles were used primarily for stabilization. This suggests the strong pronator, supinator and robust interosseus membrane in *Puijila* were important for stabilization of the manus during swimming.

In every element of the forelimb skeleton of *Puijila* there is evidence that its forelimb musculature was more specialized for swimming and likely more powerful than in *Lontra*. The actions of the enlarged teres major, deltoid, pectoralis, triceps and anconeus create flexion of the shoulder joint and extension of the elbow. These movements, combined with the extension and abduction of the digits to create an open webbed manus, would generate a powerful backwards stroke. The actions of the large supraspinatus, pectoralis, biceps and brachialis cause extension of the shoulder joint and flexion of the elbow. Combining these movements, and allowing the manus to close, would provide a strong recovery stroke. In addition, the actions of the teres major, deltoid, supraspinatus and pectoralis show the limb was capable of powerful abduction and adduction. These muscles, along with the subscapularis and infraspinatus assisted

with rotation of the humerus, indicating that the forelimb may have been capable of powerful rotary movements during swimming strokes (English, 1977). The specializations of these muscle groups in *Puijila* suggest that its forelimb was capable of creating more power, over a greater range of motion, than the limb of *Lontra*. Specifically, the enlargement of the muscles in the forelimb of *Puijila* suggests that the limb was capable of powerful backward and recovery strokes, powerful limb abduction and adduction.

Evidence from this powerful forelimb musculature may suggest behavioural specializations for swimming and/or digging. However, *Puijila* does not exhibit fossorial specializations, such as enlarged unguals. Instead the unguals are small, and the elongated digits and flattened phalanges imply the presence of webbing, suggesting that the robust forelimb musculature was primarily associated with a behavioural specialization for swimming (Rybczynski et al., 2009). This is supported by the fact that *Puijila* shows the greatest specialization in the proximal elements of the forelimb, a pattern that Savage (1957) observed in *Potamotherium* and stated was typical of an aquatically specialized animal.

The few similarities seen in the forelimb of *Puijila* and *Lontra*, particularly in the general shape of the humerus, suggest the forelimbs may have been used in similar ways during swimming. *Lontra* swims primarily using dorsoventral undulations to create propulsion with the hind feet and tail while submerged. The forelimbs are used primarily for steering underwater and for propulsion during surface swimming when the

animal employs drag-based quadrupedal paddling (Fish, 1996). However, the forelimb of *Puijila* is more specialized than that of *Lontra* and therefore it likely employed its forelimb to a greater extent while swimming than *Lontra*.

Savage (1957) postulated that the adaptations of the forelimb of *Potamotherium* indicate the limb may have been favoured for powerful “dog-paddle” swimming for periods of slower locomotion. During periods where speed was more important, they may have only been used primarily for steering, by adduction and abduction while the animal swam by pelvic undulation. This is similar to the suggestion of Rybczynski et al. (2009) that *Puijila* swam, at least in part, using quadrupedal paddling. The powerful forelimb of *Puijila* was certainly heavily involved in its swimming behaviour and the similarities in the forelimbs of *Potamotherium* and *Puijila* may indicate that *Puijila* exhibited a similar swimming behaviour to *Potamotherium*.

Although molecular phylogenetics has indicated that Pinnipedia is monophyletic, it can only provide evidence that pinnipeds are more closely related to one another than to other terrestrial arctoids. Though pinnipeds shared a common ancestor, molecular studies cannot determine the nature of that common ancestor. Pinnipeds may have diverged from a single terrestrial ancestor and become aquatic separately, or they could have had a single return to the water and originated from a semi-aquatic ancestor. Fish (1996) suggested that as a lineage evolves from being quadrupedal terrestrial animals to occupy an aquatic habitat, they first employ drag-based propulsion by quadrupedal paddling, followed by the evolution of more efficient alternate pelvic or pectoral

paddling. The two forms of aquatic locomotion in modern pinnipeds, forelimb and hind limb dominated swimming, are each specific to different extant pinniped lineages. If stem pinnipeds, like *Puijila*, did employ quadrupedal paddling as part of their aquatic locomotion, it is possible that these forms could have given rise to both of the swimming styles displayed by the modern pinnipeds.

Further understanding of the swimming mode of *Puijila* will require a detailed description of the remaining postcrania, in order to better understand the contributions that the vertebral column, pelvic girdle and hind limb had to its aquatic locomotion. The preliminary observations gained from the description of the pectoral girdle and forelimb will become more informative when they are integrated with observations from the rest of the postcrania.

SUMMARY

The comparative description of the forelimb musculoskeletal system of *Puijila* indicates it was more specialized for swimming than that of living lutrines, yet less specialized than that of *Potamotherium*. The comparative description provided here provides a basis for identifying traits of the forelimb which may be phylogenetically informative. The specializations of the forelimb of *Puijila* suggest that it was adapted to provide powerful forward and recovery strokes during swimming and its level of specialization suggests that it could have been used more frequently during aquatic propulsion than the forelimb of *Lontra*. This may indicate that quadrupedal or forelimb paddling was a more important, or a more frequently used form of locomotion in *Puijila*

than it is in modern lutrines or that *Puijila* simply used its forelimb differently than modern lutrines. Comparative descriptions of the specializations of the hind limb, pelvic girdle and vertebral column will provide insight into the role that they played in the aquatic locomotion of *Puijila*. A better understanding of the whole skeleton in a comparative framework will continue to shed light on the possible origin and evolution of the various swimming modes exhibited by modern Pinnipedia.

CHAPTER 2 - EVIDENCE FOR CORRELATED EVOLUTION BETWEEN LONG BONE

COMPACTNESS, SWIMMING BEHAVIOUR AND BODY MASS IN ARCTOIDEA

(MAMMALIA: CARNIVORA)

INTRODUCTION

Many groups of mammals have become secondarily adapted to life in water and some have achieved high levels of aquatic specialization, including the cetaceans (whales), sirenians (sea cows, dugongs) and pinnipeds (seals, sea lions and walrus) (Reidenerg, 2007; Uhen, 2007; Houssaye, 2009). The modification of internal bone microstructure to increase bone density has been hypothesized to be a specialization for aquaticism developed in these lineages (Wall, 1983; Stein, 1989; Fish and Stein, 1991; Girondot and Laurin, 2003; Laurin et al., 2004; Cubo et al., 2005; Germain and Laurin, 2005; Laurin et al., 2006; Krilloff et al., 2008; Houssaye, 2009; Canoville and Laurin, 2010). An increase in bone density through the outward thickening of cortical bone is known as pachyostosis, an inward thickening of cortical bone is osteosclerosis and the combination of both is pachyosteosclerosis (Domning and Debuffrenil, 1991; Laurin et al., 2004; Gray et al., 2007; Houssaye, 2009). However, in addition to cortical bone thickening, a bone's "compactness" can also be increased by the increased deposition of trabecular bone.

Increased bone density as a specialization for aquatic life has been studied in both modern and fossil organisms. Previous studies of modern mammals directly measured bone density by weighing bones and measuring the volume of water they

displaced when fully saturated, and then used the relationship of $\text{density} = \text{mass} / \text{volume}$ to calculate their density (Wall, 1983; Stein, 1989; Fish and Stein, 1991). Due to mineralization of bone during fossilization, these methods cannot be used to compare fossil and modern bone (Madar, 1998). An alternative approach would be to examine a bone's internal structure, which directly contributes to bone density. Wall (1983) identified that the increase in density in some of the species he examined was due to an increase in cortical bone thickness. In an attempt to compare modern and fossil bone, Madar (1998) examined cortical bone thickness by taking X-rays and using them to compare the diameter of the medullary cavity (ID) and the overall diameter (ED) at the diaphysis of the bone (Currey and Alexander, 1985; Madar, 1998). By averaging the ratio of ID/ED in anteroposterior and mediolateral directions, an average value, referred to as K, could be produced and compared between species (Currey and Alexander, 1985). However, this method did not measure increased deposition of trabecular bones which can also increase bone density, and it did not accurately represent variations in the thickness of cortical bone around the entire circumference of the section. More recently studies by Canoville and Laurin (2010), Kriloff *et al.* (2008), Germain and Laurin (2005), Laurin *et al.* (2006, 2004) have begun to examine multiple aspects of bone microstructure which might be related to aquatic specialization by using the software Bone Profiler (Girondot and Laurin, 2003). This software produces parameters that better represent a bone's compactness because they are generated by analyzing the entire section as a whole.

If bone microstructure is associated with an animal's swimming ability or behaviour, then it could provide a powerful tool to reconstruct swimming behaviour in extinct mammals. Fossil representatives of the earliest stages of the land-to-sea transition of both sirenians and cetaceans are known (Domning, 1982; Thewissen and Fish, 1997; Domning, 2001; Thewissen and Williams, 2002), but until recently there was no early morphological intermediate between swimming pinnipeds and their terrestrial ancestors represented in the fossil record. The fossil taxon that was most commonly recognized as the most basal pinniped was *Enaliarctos* (Berta et al., 1989; Berta, 1991). However, *Enaliarctos* was similar to modern pinnipeds, as it had flippers, a streamlined body, reduced limbs and was fully marine (Berta et al., 1989; Berta and Wyss, 1990; Berta, 1991). *Puijila darwini* fills the morphological gap between flippered pinnipeds and their terrestrial ancestors (Rybczynski et al., 2009). Study of the musculoskeletal specializations of the forelimb, detailed in the previous chapter, showed that *Puijila* had a greater degree of aquatic specialization than modern lutrines and likely employed its forelimbs to a greater degree than modern semi-aquatic carnivores.

This study examines the trends in bone microstructure of extant pinnipeds and their terrestrial relatives to see if they can be used as a predictive tool for reconstruction of the swimming behaviour of fossil arctoids which are suspected to be specialized for swimming. Some aquatic species within Arctoidea have been said to have elevated bone compactness, such as *Enhydra* and some pinnipeds (Wall, 1983; Fish and Stein, 1991), but the patterns of bone compactness have not been studied for this entire group.

Evidence of correlated evolution between swimming behaviour, body mass and bone microstructure in modern Arctoidea will be examined by using phylogenetically independent contrasts. The bone compactness data will also be used for predicting the swimming behaviour of the fossil stem pinniped *Puijila* using discriminant function analysis. If bone microstructure is an effective predictor of swimming behaviour, it could be a useful tool for reconstructing the changes of locomotor specializations during the early land-to-sea evolution of pinnipeds.

MATERIALS AND METHODS

Sampling Methods

A total of 43 species of arctoids were selected to represent the ecological and taxonomic diversity of the clade (Fig. 9). Each species was represented by a single male individual from the collections of the Smithsonian Institution National Museum of Natural History (USNM) (see Appendix 3). One humerus, radius, ulna, femur, tibia and fibula were analyzed from each individual. The specimens were computer tomography scanned using a Siemens Emotion Somatom flat bed scanner at the USNM. A single 1mm slice was taken at the mid-diaphysis for most elements. For pinniped humeri, which are highly derived, the scan was taken at the distal end of the deltoid crest. To standardize sampling of the ulna, the scan was taken at the midpoint of the “functional” length of the element, which did not including the length of the olecranon (Fig. 10).

The CT scan images were analyzed using Bone Profiler 4.4.11 (for Windows) to calculate the variables P, S, Min and C. Bone Profiler models a bone’s compactness by

FIGURE 9. Phylogeny showing the proposed relationships of the 43 extant arctoid species used in this study. The tree was created in Mesquite and was modified from Flynn et al. (2005), Arnason et al. (2006), Fulton and Strobeck (2006), Finarelli (2008) and Koeplifi et al. (2008). Swimming behavior categories are indicated as numbers beside species names. **Abbreviations:** *species*¹, Terrestrial (SC=0-1.49); *species*², Semi-aquatic (SC=1.5-2.99); *species*³, Aquatic (SC=3-3.99); *species*⁴, Aquatic/Semi-pelagic (SC=4).

FIGURE 10. A, position on the shaft where the bone was CT scanned and a depiction of how length measurements of the bone were taken; B, modified positioning of the CT scan location on the shaft of pinniped humeri to avoid the deltoid crest and supinator wing; C, measurements of the internal diameter of the medullary cavity (ID) and the total diameter of the bone (ED) taken from digital x-ray images to calculate the cortical bone thickness ratio $K=(ID/ED)$. **Abbreviations:** l_x , length of element x; XS, cross-section where bones were CT scanned.

dividing its cross-sectional image into 60 radial sections and then analyzing the compactness in each section from the bone's center to its edge (Girondot and Laurin, 2003). These data are graphed and a compactness curve is fitted to the data to create a compactness profile. The compactness profile is then used to produce values for the variables P, S, Min, and C that represent various aspects of the bone's microstructure (Fig. 11). The value P produced by Bone Profiler is roughly equivalent to the ratio K ($K=ID/ED$) produced from X-ray images in previous studies (Currey and Alexander, 1985; Madar, 1998; Girondot and Laurin, 2003). The variable S represents the width of the transition zone between the outer compact cortical bone and the medullary cavity. The value of Min reflects the amount and prominence of the trabeculae in the center of the section. Bone sections with thin, little or no trabeculae at their center will have a Min of zero, whereas sections with thicker, more abundant trabeculae will have higher values of Min, reflecting more bone volume towards the center of the section. Finally, C represents the overall compactness of the section and is calculated by simply dividing the number of pixels identified by the program as bone, by the total number of pixels in the section. Values of compactness at the outer edge of the section (i.e., variable referred to as "Max") were constrained to be <1 and Min was constrained to be >0 , so that calculated values of Max and Min would not exceed their theoretical maximums.

Distortion at the edges of the bone on the CT scan image increases the apparent diameter of the slice and this difference becomes more pronounced for smaller taxa. Consequently, for taxa with body mass of less than 30 kg, the long bones were digitally

X-rayed in lateral and anterior orientations using a Thermo Kevex X-Ray, model # PXS10-16W and an Amorphus-Silicon Imaging System panel. The ID and ED were measured using Vernier calipers from each digital X-Ray image and the ratio K calculated for each bone. The values of P from CT scans were compared with those of K from the X-Ray images to see if the CT scans adequately represented the true thickness of cortical bone for that species. The values were also compared to determine whether the variation in the distribution of cortical bone around the circumference of the section was properly

FIGURE 11. A representation of some of the bone microstructure parameters that are estimated from sections of bone analyzed by Bone Profiler 4.11.11. A sample compactness profile that is generated from the analysis of a bone section has been superimposed on an example bone image, to best illustrate the relationship between the parameters and the structure of an actual section. Modified from Girondot and Laurin (2003).

represented. From these comparisons, species with an average male body mass of 8 kg or higher were evaluated from CT scans using Bone Profiler and species averaging smaller than 8 kg were only represented by the K values, calculated from their X-ray images (Appendix 4). Given that K is roughly equal to P, values of K ratios calculated from X-rays were referred to in the analyses as P.

Body mass (m_b) estimates were averaged for males of each species, as reported from Walker's Mammals of the World (Nowak, 1991, 2003), Silva and Downing (1995) and Animal Diversity Web. The log of these averages ($\log(m_b)$) were used in the analyses (see Appendix 4). A continuous variable representing an animal's "swimming behaviour category" (SC) was calculated from a rubric with four categories representing a species' external aquatic specializations, diving capabilities, habitat and diet (see Appendix 5). For the purpose of some analyses, the continuous values of SC were grouped into four bins representing distinct categories of swimming behaviours: terrestrial (SC=0-1.49), semi-aquatic (SC=1.5-2.99), aquatic (SC=3-3.99), aquatic/semi-pelagic (SC=4). For some analyses the aquatic and semi-pelagic groupings were merged into a single aquatic group (SC=3-4).

Comparisons without Phylogenetic Correction

Mean values of P, S, C and Min were calculated for different swimming behaviour groups and compared. Data for the parameter P for all taxa and all bones, were imported into the data analysis package PAST 2.04 (Hammer et al., 2001). Bivariate plots of log transformed body mass ($\log(m_b)$) and the bone microstructure variable P were

constructed and ordinary least squares linear regressions were performed, to better understand the relationships between these characters without phylogenetic correction (Hammer et al., 2001).

Testing for Evidence of Correlated Evolution

Trends in bone compactness within Arctoidea may be affected by ancestry. In order to control for phylogeny, the variables SC and $\log(m_b)$ were compared pair-wise to each other and to the values of P, S, C and Min for each long bone, using Phylogenetically Independent Contrasts (PIC), calculated using the program Mesquite's PDAP:PDTREE package (Garland et al., 1993; Midford et al., 2005; Maddison and Maddison, 2006). PIC analyses use the topology of a phylogenetic tree to contrast species' character data and uses branch lengths as a measure of the expected amount of variance between these data to generate a set of independent contrasts for the character (Felsenstein, 1985; Garland et al., 1992). A significant correlation coefficient ($p\text{-value} < 0.05$) between the independent contrasts of two characters means that there is evidence of correlated evolution between those variables, independent of the influences of phylogeny. The Arctoidea tree used for PIC analyses was constructed in Mesquite and represents a strict consensus of the molecular phylogenetic trees of Flynn et al. (2005), Arnason et al. (2006), Fulton and Strobeck (2006), Finarelli (2008) and Koepfli et al. (2008) of various groups within Carnivora (Fig. 9). A full tree containing all 43 taxa was used for PIC analyses involving the variable P and a reduced tree of only the 27 larger bodied taxa whose CT scans were analyzed successfully by Bone Profiler, was used for the PIC's

involving the variables S, C and Min. Each PIC analysis was repeated four times, using four branch length algorithms provided within Mesquite. The four algorithms used were the Equivocal (all branch length equal one), the methods of Grafen (1989), those of Pagel (1992), and those of Nee as cited by Purvis (1995) (Fig. 12). To evaluate which branch length algorithms applied to the phylogenetic tree were a good fit to the tip data (SC, $\log(m_b)$, P, S, C, Min), the PDAP diagnostic chart of “Absolute contrasts vs. Standard deviation” was examined for each set of contrasts generated for each variable using each branch length method. The independent contrasts calculated from the tree topology were standardized by dividing them by the square root of their variance (or standard deviation) (Felsenstein, 1985; Garland et al., 1992). The standard deviation of a contrast is the square root of the sum of its branch lengths (Garland et al., 1992). If the independent contrasts generated for a certain branch length algorithm are adequately standardized, the slope of the least-squares linear regression between the standardized independent contrasts and their standard deviations should be significant (Garland et al., 1992; Garland et al., 1993; Midford et al., 2005). For those traits which were adequately standardized, and that correlated with both SC and $\log(m_b)$, the residuals of the linear regression of the trait (P, S, C or Min) on $\log(m_b)$ were compared with the residuals of the regression of SC on $\log(m_b)$, using an ordinary least squares regression forced through the origin, in the program PAST. These regressions can then test for relationships between SC and bone microstructure while controlling for both phylogeny and body size (Garland et al., 1992; Garland and Janis, 1993).

FIGURE 12. Phylogenies, of the 43 arctoids, showing proportional branch lengths assigned by the **A**, Equivocal; **B**, Grafen (1989); **C**, Pagel (1992); **D**, Nee algorithms.

Testing for Phylogenetic Signal

K-statistics were calculated for $\log(m_b)$, SC, P, S, C, and Min to evaluate the phylogenetic signal for each variable. The statistic was calculated using the same four branch length algorithms used in PIC analyses. K-statistic assumes Brownian motion and is another way to determine if the portion of the variance explained by a phylogenetic signal within the data is significant (Blomberg et al., 2003). A K-statistic <1 means a weak phylogenetic signal and indicates that variance in the data could be explained by correlated evolution with another character. A K-statistic > 1 indicates a strong phylogenetic signal and that variation in the data is likely explained by taxon relatedness. Values of K-statistic were calculated using the APE package for the R project for statistical computing (Blomberg et al., 2003).

Inferring the Swimming Behaviour of *Puijila darwini*

Discriminant function analysis (DFA) was performed using the JMP 9 statistical package. In this study DFA can be used to gauge the effectiveness of the continuous variables at predicting swimming behaviour category of the arctoids (terrestrial, semi-aquatic, etc.). The data for $\log(m_b)$, SC, P for all 43 taxa and $\log(m_b)$, SC, P, S, Min and C for 27 taxa were analyzed separately using linear DFA. The DFA was completed using both the original and log transformed data. When measurements of a microstructure variable yield a value of zero they were adjusted to be 10^{-7} to prevent the data from becoming undefined when log transformed. For P a value of zero implies that the medullary canal is absent. For the variable S a value of zero indicates that there was

little difference between the compactness at the outside and the inside of the bone section. Changing the original value of zero to 10^{-7} is not expected to effect interpretation of results. The DFA was then used to infer swimming behaviour for the fossil taxon *Puijila darwini*. The body mass of *Puijila* was estimated from cranial measurements using the methods of Van Valkenburgh (1990) for predicting body mass in carnivores. Body mass was estimated using the regressions for mustelids and also for ursids. The log of these two body mass estimates were used as the values for $\log(m_b)$ for *Puijila* as well as a third estimate which was simply the average of the mustelid and ursid values. Then the three estimated $\log(m_b)$ and the Bone Profiler data produced from CT scans of the long bones of *Puijila* were added to the DFA and swimming behaviour was predicted for the fossil. Finally, variables were removed from the analyses one at a time to see their effect on the classification of *Puijila*.

RESULTS

Means and Bivariate Plots

Mean values of P were calculated for three swimming categories: terrestrial (SC1), semi-aquatic (SC 2) and aquatic (SC3&4). To evaluate the difference that large body size may have on the average, the mean of only terrestrial taxa over 20 kg was also calculated. The mean of aquatic taxa was calculated excluding the semi-pelagic (SC=4) species to evaluate whether any changes in their bone microstructure associated with their long periods at sea could be affecting the average compactness for aquatic taxa. Finally, to assess whether the use of their limbs on land may have affected bone compactness, the mean compactness of otariids and walrus was calculated and compared in order to see if it differed from the mean compactness of only the phocids. The calculated means are presented in Table 3 and compared with values of P for *Puijila darwini*.

TABLE 3. Mean values of P (relative size of the medullary cavity) compared with those of *Puijila darwini*

	<u>log(m_b)</u>	<u>P_h</u>	<u>P_r</u>	<u>P_u</u>	<u>P_{fe}</u>	<u>P_t</u>	<u>P_{fi}</u>	<u>P_{for}</u>	<u>P_{hind}</u>	<u>P_{avg}</u>
Terrestrial	0.50	0.56	0.41	0.36	0.55	0.44	0.20	0.44	0.40	0.42
Terrestrial >20 kg	1.99	0.61	0.47	0.42	0.51	0.46	0.31	0.50	0.43	0.46
Semi-aquatic	1.25	0.53	0.45	0.38	0.55	0.42	0.28	0.45	0.42	0.44
Aquatic	2.46	0.47	0.55	0.46	0.59	0.47	0.43	0.49	0.50	0.50
Aquatic w/o SC4	2.40	0.42	0.52	0.41	0.54	0.44	0.39	0.45	0.45	0.45
Otariids & Walrus	2.51	0.36	0.51	0.39	0.42	0.44	0.34	0.42	0.40	0.41
Phocids	2.53	0.60	0.65	0.55	0.75	0.53	0.58	0.60	0.62	0.61
<i>Puijila (must.)</i>	0.83	0.43	0.27	0.09	0.51	0.03	0.00	0.26	0.18	0.22
<i>Puijila (ursid)</i>	1.55	0.43	0.27	0.09	0.51	0.03	0.00	0.26	0.18	0.22
<i>Puijila (avg.)</i>	1.19	0.43	0.27	0.09	0.51	0.03	0.00	0.26	0.18	0.22

(must., ursid, avg.) = Three different body mass estimates for *Puijila darwini* calculated from the regressions of Van Valkenburgh (1990). See methods.

Compared to the terrestrial group, average values of body mass are higher in semi-aquatic and aquatic groups. Mean values of P were higher (thinner cortical bone) in the humerus and femur and lower in the more distal long bones. Terrestrial taxa over 20 kg had larger values of P , or less cortical bone thickness than the average for all terrestrial taxa, except in the case of the femur. The semi-aquatic group had average values of P that were similar to the terrestrial group. The phocids had the highest average values of P . Otariids have mean values for the humerus and femur which are smaller than the terrestrial and semi-aquatic group, but higher values of the radius, ulna, tibia and fibula.

Some of the ordinary least square regressions of $\log(m_b)$ and $P_{h,u,r,fe,t,fi}$ show a significant positive correlation between P and body mass within the three swimming categories. Terrestrial arctoids showed a significant positive correlation between body mass and P_h ($r=0.52866$, $p\text{-value}=0.017$), P_u ($r=0.51302$, $p\text{-value}=0.02$) and P_{fi} ($r=0.51804$, $p\text{-value}=0.019$) (Fig. 13). Semi-aquatic arctoids showed a significant positive correlation between body mass and P_h ($r=0.90774$, $p\text{-value}=0.012$). Finally the aquatic groups showed a significant positive correlation between body mass and P_r ($r=0.69458$, $p\text{-value}=0.002$), P_u ($r=0.63233$, $p\text{-value}=0.007$) and P_{fi} ($r=0.48712$, $p\text{-value}=0.048$). The femur was the only bone to show a negative correlation within the terrestrial and semi-aquatic groupings, but the relationships were not significant. As an example of these in-group trends, Fig. 13 shows the least square regression for P_h and body mass, of which the terrestrial and semi-aquatic groups have significant positive correlations.

FIGURE 13. Example plots of P_h and $\log(m_b)$ for each swimming behaviour group illustrating the positive trends within groups. (Terrestrial: SC=0-1.49; Semi-aquatic: SC=1.5-2.99; Aquatic: SC=3-4), phocids are identified by dark blue stars overlaid on their aquatic data points.

Phylogenetically Independent Contrasts

The four branch-length algorithms (Equivocal, Grafen (1989), Pagel (1992), Nee) were tested for which produced adequately standardized independent contrasts for each character (Tables 4, 5). The character $\log(m_b)$ was adequately standardized using any of all branch length algorithms on both the full ($n=43$) and reduced ($n=27$) trees. The trait SC was not adequately standardized using the Equivocal branch length algorithm on the full tree, but was for all other branch length algorithms applied to the full or reduced trees. The variable P showed significantly negative slopes for a minimum of six

characters for all four branch length algorithms on the full tree, indicating that branch lengths were a poor fit for the tip data in most cases (Midford et al., 2005). Log transformation of branch length, shrinks long branches relative to short ones, and is recommended to help standardize contrasts when non-transformed branch lengths produce a plot of independent contrast vs standard deviations with a significantly negative slope (Garland et al., 1992). Natural log transformations of branch lengths for the algorithms of Grafen (1989) and Pagel(1992), without first multiplying by a constant, resulted in the collapsing of several nodes into polytomies. Natural log transformation of the branch lengths assigned by the Nee algorithm, produced adequately standardized independent contrasts for the variable P (Table 4).

Adequately standardized independent contrasts were produced for the trait S using the branch lengths produced from the Equivocal, Grafen (1989) and Nee methods (Table 5). The contrasts for the character Min were standardized when branch lengths were produced using the Grafen (1989), Pagel (1992), and Nee methods (Table 5). The results of correlations between the independent contrasts of $\log(m_b)$ and SC and those of bone microstructure P, S and Min, were only considered for the branch lengths for which they were adequately standardized.

TABLE 4. Pearson product-moment correlation coefficients of the plot of absolute values of the independent contrasts of P vs. standard deviations for branch length algorithms applied to the full tree (43 species). Significant p-values < 0.05 represent inadequate standardization of contrasts.

	Equivocal			Grafen (1989)			Pagel (1992)			Nee			ln(Nee)		
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	
SC	0.307	0.048	0.05	0.767	-0.01	0.939	0.099	0.532	0.034	0.831					
log(m _b)	0.237	0.131	-0.268	0.086	-0.115	0.462	-0.035	0.825	-0.100	0.534					
P _h	-0.188	0.232	-0.360	0.020	-0.369	0.016	-0.307	0.048	-0.154	0.332					
P _r	-0.390	0.011	-0.529	3.20*10 ⁻⁴	-0.552	1.52*10 ⁻⁴	-0.514	4.94*10 ⁻⁴	-0.162	0.305					
P _u	-0.306	0.049	-0.384	0.012	-0.413	0.007	-0.386	0.012	-0.216	0.170					
P _{fe}	-0.142	0.368	-0.403	0.008	-0.407	0.008	-0.274	0.079	-0.046	0.771					
P _t	-0.312	0.044	-0.433	0.004	-0.457	0.002	-0.387	0.011	-0.238	0.128					
P _{fi}	-0.343	0.026	-0.465	0.002	-0.509	5.84*10 ⁻⁴	-0.497	8.10*10 ⁻⁴	-0.215	0.171					
P _{for}	-0.347	0.024	-0.448	0.003	-0.495	8.59*10 ⁻⁴	-0.469	0.002	-0.114	0.471					
P _{hind}	-0.310	0.046	-0.476	0.001	-0.514	4.91*10 ⁻⁴	-0.455	0.002	-0.229	0.144					
P _{avg}	-0.250	0.110	-0.423	0.005	-0.456	0.002	-0.405	0.008	-0.113	0.477					

Bold indicates p-values that are < 0.05.

TABLE 5. Pearson product-moment correlation coefficients of the plot of absolute values of the independent contrasts of S and Min vs. standard deviations for branch length algorithms applied to the reduced tree (27 largest species). Significant p-values < 0.05 represent inadequate standardization of contrasts.

	Equivocal			Grafen (1989)			Pagel (1992)			Nee		
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value
SC	0.189	0.355	-0.005	0.981	0.146	0.476	0.287	0.155				
log(m _b)	0.240	0.237	-0.190	0.354	-0.159	0.438	0.040	0.848				
S _h	-0.272	0.179	-0.341	0.088	-0.331	0.098	-0.226	0.267				
S _r	0.022	0.914	-0.313	0.119	-0.396	0.045	-0.216	0.289				
S _u	-0.065	0.751	-0.378	0.057	-0.394	0.047	-0.196	0.337				
S _{fe}	0.141	0.493	-0.286	0.156	-0.270	0.182	-0.073	0.724				
S _t	-0.130	0.527	-0.335	0.095	-0.447	0.022	-0.272	0.180				
S _{fi}	0.121	0.556	-0.09	0.648	0.138	0.503	0.101	0.621				
S _{for}	-0.198	0.332	-0.357	0.074	-0.424	0.031	-0.317	0.114				
S _{hind}	-0.121	0.556	-0.341	0.088	-0.388	0.050	-0.250	0.219				
S _{avg}	-0.233	0.452	-0.330	0.087	-0.402	0.054	-0.286	0.172				
Min _h	0.200	0.327	-0.134	0.513	-0.078	0.704	0.068	0.742				
Min _r	0.447	0.022	0.159	0.439	0.292	0.148	0.373	0.060				
Min _u	-0.155	0.449	-0.255	0.208	-0.348	0.081	-0.287	0.155				
Min _{fe}	0.393	0.047	0.211	0.302	0.307	0.127	0.372	0.061				
Min _t	0.290	0.150	-0.043	0.831	0.112	0.585	0.213	0.296				
Min _{fi}	0.058	0.521	-0.123	0.607	0.067	0.628	0.084	0.580				
Min _{for}	0.094	0.647	-0.190	0.353	-0.247	0.223	-0.102	0.618				
Min _{hind}	0.087	0.248	-0.135	0.708	-0.096	0.479	0.134	0.358				
Min _{avg}	0.027	0.264	-0.236	0.501	-0.050	0.979	0.012	0.618				

Bold indicates p-values that are < 0.05.

TABLE 6. Pearson product-moment correlation coefficients of the plot of absolute values of the independent contrasts of C vs. standard deviations for branch length algorithms applied to the reduced tree (27 largest species). Significant p-values < 0.05 represent inadequate standardization of contrasts.

	Equivocal			Grafen (1989)			Pagel (1992)			Nee			ln(Nee)		
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	
SC	0.189	0.355	-0.005	0.981	0.146	0.476	0.287	0.155	0.362	0.069					
log(m _b)	0.240	0.237	-0.190	0.354	-0.159	0.438	0.040	0.848	0.104	0.614					
C _h	-0.373	0.060	-0.404	0.041	-0.468	0.016	-0.429	0.029	0.328	0.102					
C _r	-0.421	0.032	-0.542	0.004	-0.637	4.71*10 ⁻⁴	-0.534	0.005	-0.515	0.007					
C _u	-0.430	0.028	-0.402	0.042	-0.534	0.005	-0.497	0.010	-0.441	0.023					
C _{fe}	-0.113	0.580	-0.298	0.139	-0.345	0.085	-0.210	0.302	-0.108	0.599					
C _t	-0.288	0.154	-0.423	0.031	-0.499	0.009	-0.396	0.045	-0.308	0.125					
C _{fi}	-0.359	0.072	-0.402	0.042	-0.533	0.005	-0.485	0.012	-0.407	0.039					
C _{for}	-0.472	0.015	-0.467	0.016	-0.584	0.002	-0.557	0.003	-0.504	-0.009					
C _{hind}	-0.315	0.117	-0.404	0.041	-0.538	0.005	-0.442	0.024	-0.340	0.08					
C _{avg}	-0.377	0.058	-0.426	0.030	-0.548	0.004	-0.495	0.010	-0.421	0.032					

Bold indicates p-values that are < 0.05.

Finally, the contrasts for the character C were not adequately standardized for every bone by using a single Branch length algorithm (Table 6). The equivocal branch length method adequately standardized all but C_r , C_u and C_{for} . The equivocal branch length method was used for correlations between the independent contrasts of SC and $\log(m_b)$ and the results of these correlations were only reported from those variables which were adequately standardized (i.e., C_h , C_{fe} , C_t , C_{fi} , C_{hind} , and C_{avg}).

Tables 7 to 11 show the correlation coefficients, and their associated two-tailed p-values, describing the relationship between each bone microstructure variable and body mass or SC using standardized independent contrasts. Body mass and swimming behaviour showed evidence of correlated evolution for all branch length methods ($n=43$, $n=27$) (Table 7, 8).

TABLE 7. Pearson product-moment correlation coefficients (r) and their associated two-tailed p-values of the independent contrasts of $\log(m_b)$ vs. independent contrasts of SC, calculated from four different branch length algorithms applied to the reduced tree ($n=27$).

	r	p-value
Equivocal	0.606	8.04×10^{-4}
Grafen (1989)	0.558	0.002
Pagel (1992)	0.601	9.08×10^{-4}
Nee	0.545	0.003

Bold indicates a significant correlation with 2-tailed p-values <0.05

The variable P_{fi} and P_{avg} covaried with SC and P_h , P_u , P_{for} and P_{avg} covaried with $\log(m_b)$ ($n=43$) (Table 8). The character S showed no relationship with SC. When branch lengths were set to be equivocal, S_r , S_u , S_t , S_{fi} , S_{for} and S_{avg} had evidence of a relationship with $\log(m_b)$. When the branch length algorithms of Grafen (1989) were used S_r and S_t

had evidence of a relationship with $\log(m_b)$. Finally, when using the branch lengths produced by the Nee method, S_r , S_t and S_{for} had evidence of a relationship with $\log(m_b)$ ($n=27$) (Table 9). There was no relationship between Min and SC and only Min_{fe} covaried with $\log(m_b)$ for each of Grafen (1989), Pagel (1992) and Nee branch length algorithms ($n=27$) (Table 10). Finally, C covaried significantly with SC and $\log(m_b)$. When branch lengths were set to be equivocal, C_{fi} had a relationship with SC ($n=27$). The bone microstructure character C_{fe} , C_{fi} , C_{hind} and C_{avg} had a negative correlation with $\log(m_b)$ using the equivocal branch length method ($n=27$) (Table 11).

TABLE 8. Pearson product-moment correlation coefficients (r) and their associated two-tailed p-values produced as a result of Phylogenetically Independent Contrasts of P with SC and $\log(m_b)$ using a natural log transformed Nee branch length algorithm ($n=43$).

	SC		$\log(m_b)$	
	<u>r</u>	<u>p-value</u>	<u>r</u>	<u>p-value</u>
SC	NA	NA	0.488	8.97×10^{-4}
$\log(m_b)$	0.488	8.97×10^{-4}	NA	NA
P_h	0.168	0.282	0.312	0.041
P_r	0.298	0.052	0.281	0.068
P_u	0.286	0.063	0.406	0.007
P_{fe}	0.300	0.051	0.185	0.235
P_t	0.123	0.431	0.121	0.439
P_{fi}	0.328	0.032	0.276	0.073
P_{for}	0.292	0.057	0.388	0.010
P_{hind}	0.291	0.058	0.232	0.134
P_{avg}	0.315	0.040	0.336	0.027

Bold indicates a significant correlation with 2-tailed p-values <0.05

TABLE 9. Pearson product-moment correlation coefficients (r) and their associated two-tailed p -values produced as a result of Phylogenetically Independent Contrasts of S with SC and $\log(m_b)$ using three different branch length algorithms ($n=27$).

	Grafen (1989)						Nee					
	Equivocal			SC			SC			$\log(m_b)$		
	r	p -value	$\log(m_b)$	r	p -value	$\log(m_b)$	r	p -value	$\log(m_b)$	r	p -value	$\log(m_b)$
S_h	0.372	0.056	0.254	0.200	0.438	0.145	0.472	0.335	0.087	0.252	0.204	
S_r	0.301	0.127	0.486	0.010	0.345	0.433	0.024	0.249	0.210	0.482	0.011	
S_u	0.247	0.214	0.384	0.048	0.747	0.229	0.251	0.148	0.462	0.353	0.071	
S_{fe}	0.326	0.098	0.277	0.163	0.687	0.000	1.000	0.244	0.220	0.189	0.344	
S_t	0.285	0.150	0.464	0.015	0.444	0.459	0.016	0.217	0.268	0.456	0.017	
S_{fi}	-0.227	0.255	-0.420	0.029	0.227	-0.278	0.160	-0.258	0.194	-0.309	0.117	
S_{for}	0.373	0.056	0.463	0.015	0.424	0.317	0.107	0.294	0.137	0.442	0.021	
S_{hind}	0.296	0.134	0.296	0.134	0.890	0.094	0.641	0.195	0.331	0.242	0.225	
S_{avg}	0.283	0.072	0.326	0.042	0.830	0.193	0.335	0.189	0.345	0.308	0.118	

Bold indicates a significant correlation with 2-tailed p -values < 0.05

TABLE 11. Pearson product-moment correlation coefficients (r) and their associated two-tailed p-values produced as a result of Phylogenetically Independent Contrasts of C with SC and $\log(m_b)$ using equivocal branch lengths ($n=27$). The independent contrasts of C_r , C_u and C_{for} were not adequately standardized and so their results are omitted.

	SC		$\log(m_b)$	
	r	P-value	r	P-value
C_h	-0.133	0.510	-0.315	0.110
C_r	NA	NA	NA	NA
C_u	NA	NA	NA	NA
C_{fe}	-0.367	0.060	-0.394	0.042
C_t	-0.221	0.267	-0.191	0.340
C_{fi}	-0.443	0.021	-0.488	0.010
C_{for}	NA	NA	NA	NA
C_{hind}	-0.380	0.050	-0.397	0.041
C_{avg}	-0.351	0.072	-0.472	0.013

Bold indicates a significant correlation with 2-tailed p-values <0.05

For those characters that covaried with both SC and $\log(m_b)$ the residuals of the regression of their standardized independent contrasts on the positivized contrasts of $\log(m_b)$ were plotted against the residuals of the regression of the independent contrasts of SC on those of $\log(m_b)$. The bi-variate plots of those residuals, with the ordinary least squares regression line forced through the origin, are shown in Fig. 14. None of the bone microstructure variables retained a significant Pearson correlation coefficient (r) with SC , when their residuals were plotted to control for phylogeny and body mass.

FIGURE 14. A) The residuals of the independent contrasts, standardized using Equivocal branch lengths, of C_{fi} vs $\log(m_b)$ plotted against those of SC vs $\log(m_b)$ with the trend line of the ordinary least square regression through the origin. ($n=27$, $r=-0.20115$, $p\text{-value}=0.32445$); B) The residuals of the independent contrasts, standardized using $\ln(N_{ee})$ branch lengths, of P_{avg} vs $\log(m_b)$ plotted against those of SC vs $\log(m_b)$ ($n=43$, $r=0.19435$, $p\text{-value}=0.21746$)

It has been hypothesized that cortical bone thickness is related to the requirements of terrestrial animals to support their mass on land (Currey and Alexander, 1985; Egi, 2001). Phocids do not use their limbs on land for structural support and they have large average body masses, so they were removed from the PIC analysis of the character P in order to evaluate whether the group might be influencing the positive relationship between P and $\log(m_b)$. When the two species of phocids that had the highest possible SC scores (SC=4) were removed from the data set, all relationships between SC and P were lost and $\log(m_b)$ only showed a relationship with P_u (n=41) (Table 12). The natural log transformed Nee method remained adequate for standardizing all characters on the 41 taxa (no SC 4) tree. When all eight species of phocids were removed from the analysis, all evidence of correlated evolution between P and SC, and between P and $\log(m_b)$ were lost (n=35). The natural log transformed branch lengths produced by the Nee method still performed the best of all the branch length methods in diagnostic tests, but P_t was no longer adequately standardized on the 35 taxa (no phocid) tree. Therefore, the coefficient of correlation and associated p-value were not examined for the results. The PIC analysis involving S, C and Min were not repeated with the exclusion of phocids as that would have resulted in an analysis with only 19 taxa and the small data set would have been less informative about overall trends in Arctoidea. In all analyses SC and $\log(m_b)$ showed evidence of correlated evolution.

TABLE 12. Pearson product-moment correlation coefficients (r) and their associated two-tailed p-values produced as a result of Phylogenetically Independent Contrasts of P with SC and $\log(m_b)$ using a natural log transformation Nee branch length algorithm. Results were calculated excluding species with an SC=4 (n=41).

	SC		$\log(m_b)$	
	r	p-value	r	p-value
SC	NA	NA	0.444	0.004
$\log(m_b)$	0.444	0.004	NA	NA
P _h	-0.038	0.815	0.177	0.269
P _r	0.218	0.171	0.192	0.230
P _u	0.126	0.432	0.337	0.032
P _{fe}	0.157	0.325	0.010	0.949
P _t	1.03×10^{-4}	0.999	0.019	0.904
P _{fi}	0.219	0.169	0.161	0.313
P _{for}	0.144	0.369	0.295	0.061
P _{hind}	0.152	0.342	0.092	0.568
P _{avg}	0.170	0.287	0.220	0.168

Bold indicates p-values that are significant (<0.05).

Phylogenetic Signal

K-statistic results show there is very little phylogenetic signal in the bone microstructure character data (P, S, C and Min) for all long bones, but that SC and $\log(m_b)$ contain a strong phylogenetic signal (Table 13). The compactness of the femur showed evidence of a strong phylogenetic signal in one instance when using the Nee branch length algorithm.

TABLE 13. All values of K-statistic calculated using the APE package for the R project for statistical computing. K-statistic <1 indicates a weak phylogenetic signal and K-statistic >1 indicated a strong phylogenetic signal.

<u>Equivocal Branch Lengths</u>					<u>Grafen Branch Lengths</u>				
$\log(m_b)^*$ -		1.48	SC* -		0.76		SC* -		1.08
$\log(m_b)$ -		1.36	SC -		0.58		SC -		0.9
	P*	S	C	Min		P*	S	C	Min
Humerus	0.43	0.68	0.42	0.57	Humerus	0.1	0.24	0.13	0.24
Radius	0.4	0.67	0.51	0.64	Radius	0.12	0.22	0.17	0.41
Ulna	0.34	0.61	0.33	0.41	Ulna	0.08	0.22	0.1	0.14
Femur	0.75	0.86	0.83	0.66	Femur	0.21	0.3	0.3	0.49
Tibia	0.34	0.7	0.45	0.5	Tibia	0.08	0.23	0.15	0.25
Fibula	0.52	0.4	0.48	0.33	Fibula	0.15	0.16	0.15	0.15
Forelimb	0.36	0.69	0.37	0.55	Forelimb	0.09	0.21	0.11	0.2
Hindlimb	0.49	0.69	0.57	0.38	Hindlimb	0.13	0.22	0.19	0.17
All	0.44	0.71	0.46	0.46	All	0.11	0.22	0.14	0.19

<u>Pagel Branch Lengths</u>					<u>Nee Branch Lengths</u>				
$\log(m_b)^*$ -		1.54	SC* -		2.48		SC* -		2.89
$\log(m_b)$ -		1.23	SC -		1.58		SC -		1.82
	P*	S	C	Min		P*	S	C	Min
Humerus	0.27	0.63	0.35	0.59	Humerus	0.56	0.81	0.51	0.72
Radius	0.3	0.55	0.48	0.84	Radius	0.62	0.76	0.65	0.87
Ulna	0.21	0.57	0.28	0.38	Ulna	0.46	0.75	0.42	0.55
Femur	0.5	0.72	0.78	0.92	Femur	0.96	0.91	1.04	0.9
Tibia	0.19	0.59	0.4	0.59	Tibia	0.43	0.82	0.59	0.69
Fibula	0.37	0.46	0.42	0.42	Fibula	0.79	0.58	0.61	0.5
Forelimb	0.23	0.57	0.32	0.51	Forelimb	0.5	0.77	0.47	0.7
Hindlimb	0.31	0.59	0.51	0.47	Hindlimb	0.66	0.79	0.73	0.55
All	0.28	0.6	0.4	0.5	All	0.61	0.8	0.58	0.61

* indicates results calculated with the full 43 taxa tree

Bold indicates a strong phylogenetic signal.

Linear Discriminant Function Analysis

Results of linear discriminant function analysis (DFA) of the original values for P for all 43 taxa as well as $\log(m_b)$ incorrectly classified 11.63% of species within the four swimming behaviour category bins (terrestrial=1, semi-aquatic=2, aquatic=3, semi-pelagic=4). Log transforming the data for P improved the results to only 9.302%, or four of 43 species misclassified. Ursids were often misclassified as semi-aquatic and when this group is removed from the analysis the percent of misclassified species drops to 2.564% with non-transformed data. However, when $\log(m_b)$ is excluded from the analysis the percent of misclassified species increases to 16.28% with original data and 34.88% with log transformed data. When swimming categories were further simplified into 3 bins (terrestrial=1, semi-aquatic=2 and aquatic=3), by including the semi-pelagic forms in the aquatic group, the number of misclassified species increased to 13.95% for non-transformed data and remained constant at 9.032% for log transformed data.

When the original data for S, C, and Min, for the 27 larger taxa, and $\log(m_b)$ are included together in a linear DFA only 3.704% of species are misclassified. When the data is log transformed this improved to 100% of species correctly classified. When the values of P are also included for these 27 species, it produces a singular in the covariance matrix as the number of variables is greater than the number of species to be classified. Therefore, P was omitted from the DFA's which used 27 species.

Body mass estimates for *Puijila darwini* were produced using regressions of log transformed cranial measurements and log transformed body mass from Van

Valkenburgh (1990). Estimates were produced using three different cranial measurements and the regressions from the families Ursidae and Mustelidae. This gave three estimates of $\log(m_b)$ for *Puijila* of 0.83 as a mustelid, 1.51 as an ursid and an average of these two values of 1.19. These translate to body mass estimates of approximately 7 kg, 32 kg and 16 kg respectively. When *Puijila* was compared to the modern taxa in analyses which included body mass, it was consistently predicted to belong to either the semi-aquatic or aquatic bins. In DFA, where the estimated body masses were not used, *Puijila* was more often predicted to belong to the semi-aquatic swimming behaviour grouping (Table 14).

When variables were removed one at a time from DFA which included the variables $\log(m_b)$ and P_t , *Puijila* retained his classification as a swimming arctoid (SC=2 or 3) as long as $\log(m_b)$ was present. When $\log(m_b)$ was not included in the DFA, the removal of P_t or $\log(P_t)$ caused *Puijila* to be reclassified as terrestrial instead of semi-aquatic or aquatic. This remained true in analyses where SC 4 taxa were included with SC 3 in a single grouping. This indicates that log body mass is important for the classification of *Puijila* as swimming arctoid, but that the values of cortical bone thickness of the tibia also contribute to its designation. However, the tibia does not classify *Puijila* as terrestrial in the absence of $\log(m_b)$ in analyses where ursids are not included.

The removal of body mass does not effect the classification of *Puijila* as a swimming arctoid for analyses involving S, C and Min. Removing of any one variable, or

group of variables (S, C or Min) does not classify *Puijila* as terrestrial.

TABLE 14. Results of the predicted swimming behaviour for *Puijila darwini* using linear Discriminant Function Analysis.

Species (n =)	SC bins (X, categories)	Y, covariates	% misclassified	<i>Puijila</i> (m, u, avg.)	Probability (m, u, avg.)
43	1,2,3,4	log(m _b), P	11.630	2, 3, 2	0.87, 0.74, 0.62
43	1,2,3	log(m _b), P	13.950	2, 2, 2	0.95, 0.89, 0.95
39*	1,2,3,4	log(m _b), P	2.564	2, 3, 2	0.966, 0.931, 0.592
43	1,2,3,4	log(m _b), log(P)	9.302	3, 3, 3	0.986, 0.999, 0.996
43	1,2,3	log(m _b), log(P)	9.302	3, 3, 3	0.651, 0.969, 0.884
43	1,2,3,4	P	16.280	2	0.819
43	1,2,3,4	log(P)	34.880	2	0.455
39*	1,2,3,4	P	12.820	2	0.916
27	1,2,3,4	log(m _b), S, C, Min	3.704	3, 3, 3	1.00
27	1,2,3,4	log(m _b), log(S), log(C), log(Min)	0.000	2, 2, 2	1.00
27	1,2,3,4	S, C, Min	3.704	3	1.00
27	1,2,3,4	log(S), log(C), log(Min)	0.000	2	1.00

* - indicates data sets which excluded ursids;
(m,u,avg.) – indicates the predicted SC and its probability, based on the three different body mass estimates for *Puijila darwini*.

DISCUSSION

When discussing hypotheses of correlated evolution between limb bone density and swimming behaviour, it is important to recognize that changes in bone microstructure are driven by more than simply selective pressure for increased limb bone density to counter an animal's natural buoyancy. Long bones must be able to withstand the stress and strain associated with supporting their body on land during locomotor and other activities. Each animal requires a different optimal balance of cortical bone thickness and shaft diameter to achieve its equilibrium (Currey and Alexander, 1985). These functional requirements mean that bone microstructure should be heavily influenced by an animal's body mass. This should be especially true for terrestrial animals which must constantly support their entire weight on their limbs, without the aid of water, to help support their mass. Those animals which have become fully pelagic, such as modern cetaceans, are free of the structural constraints on their bone microstructure that arise from the use of limbs on land, though they would still be subject to the influence of the stress and strain on their limb bones which would arise from aquatic locomotion. Bone shape is also influenced by the need to provide attachment for the muscles which are involved in aquatic locomotion.

Influence of Body Mass on Cortical Bone Thickness

Pinnipeds are the most aquatic arctoids, yet they are not as aquatically specialized as some mammalian lineages such as cetaceans and sirenians. Otariids and odobenids continue to use some or all of their limbs on land, so it would be expected

that the microstructure of the limb bones of these taxa retain evidence that the limb is used to support their weight. Therefore, body mass should still have some influence on the bone microstructure even in these aquatic arctoid taxa.

In a study that investigated the relationships between body mass and skeletal measurements of the humerus, femur and tibia of recent carnivores, Egi (2001) found that humeral and femur cortical cross-sectional areas were better predictors of body mass than the length or articular surface area of those bones. When the cortical bone thickness ratios (P) of the humerus and femur of the 43 arctoids in this study are plotted as one group with body mass, and an ordinary least squares regression is performed, there is no correlation between the variables (humerus: $r=-0.009261$, $p\text{-value}=0.953$; femur: $r=0.07643$, $p\text{-value}=0.626$). However, when the species are divided into their swimming category bins (terrestrial, semi-aquatic and aquatic) there is a significant positive correlation between body mass and the humerus of terrestrial and semi-aquatic species (terrestrial: $r=0.52866$, $p\text{-value}=0.0166$; semi-aquatic: $r=0.90774$, $p\text{-value}=0.012$), but not with the femur. A higher value of P corresponds to a larger medullary cavity and less compact bone (Currey, 2003; Girondot and Laurin, 2003). The positive correlations within swimming behaviour groups are opposite of the observations of Egi (2001) that larger taxa had larger cortical bone area. The difference in results may be related to differences in the taxa sampled. In comparison to this study, Egi (2001) used only relatively small terrestrial carnivorous mammals in his body mass study (i.e. less than 25 kg). Another study that included larger and more taxonomically diverse terrestrial

mammals in their analysis found poor correlation coefficients between body mass and cortical bone thickness (Currey and Alexander, 1985).

Currey and Alexander (1985) examined the mechanical properties of tubular long bones. They calculated ratios of P that would be optimal for minimizing weight while also providing the greatest impact strength when loaded. The ratio $P=0.55$ would be the theoretical optimum for terrestrial organisms' long bones to have ultimate strength and to best withstand impact loading, while minimizing weight, thus saving energy. Their examination of modern terrestrial mammals ranging in size from 2500 kg to 0.0057 kg, revealed that this theoretical value was very close to the average values for the humeri and femora, but that more distal bones tended to be more compact than the optimum. They observed larger taxa tended to have lower values of P than smaller taxa. In their study of 28 taxonomically diverse, terrestrial mammals, actual correlations between cortical bone thickness and body mass revealed that the only major long bone to show a significant negative correlation was the femur. They also stated that larger values of P would be expected in taxa which had high selective pressure for weight reduction; an extreme example of which would be flying birds. Currey and Alexander (1985) did not investigate the relationship of body mass and cortical bone thickness in aquatic and semi-aquatic mammals; including only one sirenian as a representative in their analysis which are well known to have highly pachyostotic bones.

The terrestrial and semi-aquatic artiodactyls examined for this study display an average value of P that corresponds to the theoretical value for impact loading. They

also conform to the previously observed trend (Currey and Alexander, 1985) that more distal long bones tend to be more compact than the optimum for impact loading. The relationship between P and body mass with arctoids and within each swimming behavioural grouping is positive for most bones, indicating that larger arctoids tend to have less compact bones than smaller arctoids. This seems counter to the predictions of Currey and Alexander (1985).

Other bone density studies found higher cortical bone thickness and compactness occur often in aquatic taxa; sometimes found in modern lineages (eg. sirenians) or ancestral fossil forms (eg. cetaceans) (Domning and Debuffrenil, 1991; Madar, 1998; Laurin et al., 2004; Thewissen et al., 2007; Houssaye, 2009; de Buffrenil et al., 2010). The mean values of the cortical bone thickness ratio (P) for aquatic arctoids in this study are larger than the terrestrial group and thus do not appear to follow these patterns. By excluding phocids from the mean, so that only aquatic arctoids that still use their limbs to support their weight on land are considered, the resulting value of P conforms more to the predictions of Currey and Alexander (1985). The values for the humerus and femur of non-phocid aquatic taxa are more compact than their terrestrial relatives and distal bones are less or equally compact. The average P for non-phocid aquatic taxa is slightly smaller than the average for the larger terrestrial taxa, though they also have higher average body mass. Phocid taxa have average less cortical bone thicknesses than terrestrial arctoids and they do not use their limbs to support their body weight on land.

The shift to a relatively more compact humerus and femur in otariids and *Odobenus* could be related to the shortening of those bones. However, when the log transformed length of these bones were plotted against their cortical bone thickness ratio in an ordinary least squares regression, there was no apparent relationship between the characters (humerus: $r=0.090224$, $p\text{-value}=0.56503$; femur: $r=-0.028272$, $p\text{-value}=0.85718$). Even when the large values of P displayed by phocids are removed from the regression, there continues to be no significant relationship between cortical bone thickness and the length of the element (humerus: $r=0.19308$, $p\text{-value}=0.28969$; femur: $r=-0.1641$, $p\text{-value}=0.36974$). Otariids and *Odobenus* retain a positive relationship between P and body mass. Therefore, it appears that within Arctoidea in general there is a decrease in cortical bone thickness with increasing body mass. This could be a result of selective pressure to optimize, and reduce where possible, an animal's body mass, and therefore the metabolic costs of locomotion (Currey and Alexander, 1985).

Bone Microstructure and Swimming Behaviour

Recent studies of bone microstructure in aquatic animals have often used linear measurements as an approximation of body size to compare with bone microstructure (Girondot and Laurin, 2003; Laurin et al., 2004; Cubo et al., 2005; Germain and Laurin, 2005; Laurin et al., 2006; Krilloff et al., 2008; Canoville and Laurin, 2010). However, an animal's size or length does not always accurately predict its actual body mass. Two animals of the same presacral length may have vastly different body masses. This is evident from attempts to predict body mass in fossil taxa by using linear regressions on

skeletal measurements and body mass data of modern taxa (Van Valkenburgh, 1990).

Regressions at the family level yield more accurate results than regressions at larger taxonomic groupings. This indicates there is a phylogenetic component to the relationship between skeletal measurements and body mass, and suggests that tetrapods from disparate lineages with similar body lengths may have very different body masses. This is supported by k-statistic results of this study, which found that both body mass and swimming behavioural data of the 43 arctoid species contained a strong phylogenetic signal. Therefore, examining the relationship between presacral length, or other linear body measurements, and bone microstructure may not be effective at representing the effect that an animal's mass has on bone microstructure, especially in taxonomically diverse data sets.

Previous studies using Bone Profiler have shown evidence of body size (using length measurements) correlating with certain aspects of bone microstructure and swimming behaviour in tetrapod groups. Laurin *et al.* (2004) found that body size and femur compactness both increased in aquatic lissamphibians, and Cubo *et al.* (2006) discovered correlated evolution between body size and swimming behaviour in sauropsids. Germain and Laurin (2005) found that the maximal diameter of the radius tended to be larger in aquatic amniotes. Canoville and Laurin (2010) discovered that body size measurements such as presacral length and bone diameter showed evidence for correlated evolution with swimming when compared using PIC analyses within amniotes. They did not specifically examine the relationship between body mass and

bone microstructure variables in their analyses.

The results of this study show a relationship between body mass and bone microstructure. For the variables *S* and *Min* there is no evidence for correlated evolution with swimming behaviour, and only evidence of correlated evolution between *S* and *Min* of certain long bones, with body mass. The character *S* is related to the width of the transition zone between cortical bone and the trabecular bone of the medullary cavity (Girondot and Laurin, 2003). The variable *S* showed positive correlations with body mass indicating that as arctoids become larger the transition between medullary cavity and cortical bone becomes more gradual. Bone density near the center of the cross section (*Min*) shows a positive relationship with body size ($\log(m_b)$) for the femur. The parameter *Min* is influenced by the prominence and quantity of trabeculae in the medullary cavity (Girondot and Laurin, 2003; Laurin et al., 2004). The positive relationship between body mass and *Min* suggests that as body mass increases in arctoids there is an increase of deposition of trabecular bone, increasing the prominence of the trabeculae in the femur.

The variables describing overall compactness (*C*) and medullary size (*P*) show evidence of correlated evolution with both body mass and swimming behaviour for some long bones. Only *C_{fi}* correlated with swimming behaviour, but the variable is also correlated with body mass. The variable *P* correlated with swimming behaviour and also consistently correlated with body mass for most of the long bones. The exception is *P_{fi}*, which correlated with swimming behaviour and not body mass. The analysis included

many pinniped species; many that do not support their full body weight with their hind limbs (Howell, 1929; Demere et al., 2003; Bebej, 2008). Not using their hind limbs for support on land may reduce the constraints that body mass places on the evolution of cortical bone thickness in these elements and could be a reason for a lack of a relationship between P_{fi} and $\log(m_b)$. This suggests that in arctoids, the cortical bone thickness of the fibula may be less influenced by body mass than other elements and could be a better predictor of swimming behaviour. However, these results are to be taken with caution, because the fibula is the smallest bone in the sample and therefore more susceptible to measuring errors and CT scan distortion. Also, the small size of the fibula limits the impact that increasing its compactness would have on overall buoyancy control. Also, when phocids are removed from the analysis all relationships between long bone cortical bone thickness and swimming behaviour are lost, including those of P_{fi} and SC. This indicates that the correlation between P_{fi} and SC is being driven by these large bodied aquatic taxa and that the relationship might not be an effective predictor for classifying smaller bodied transitional fossil arctoids that are semi-aquatic or terrestrial.

A combination of soft tissue specializations for swimming and diving and a decrease in the use of their limbs for structural support on land can create a scenario where cortical bone thickness decreases in aquatic taxa, a pattern seen in cetaceans (Gray et al., 2007). Phocids do not rely on any of their limbs to support their weight on land and in swimming use their hind feet for propulsion and their forelimbs for steering

and stability (Howell, 1929; Bebej, 2008). Therefore, there should be fewer constraints from body mass on cortical bone thickness in this group. When phocids are removed from PIC analyses of P, the positive relationships between medullary size of the long bones and swimming behaviour are no longer significant, suggesting that phocids are driving the trends in cortical bone thickness in arctoids.

The results of the PIC analyses in this study indicate that swimming behaviour and body mass were positively correlated. It is possible that the relationship seen between swimming behaviour and certain long bone compactness variables could simply be due to the larger average size of the aquatic and semi-aquatic arctoids. When the residuals of the characters that showed a relationship to both swimming behaviour and body mass (C, P) are plotted against the residuals of swimming behaviour and body mass, to remove the influence of body mass as well as phylogeny, the relationship between these characters and swimming behaviour is lost in all cases. This suggests that the evidence of correlated evolution between bone microstructure traits (P, C) and swimming behaviour is driven by their relationship with body mass. Therefore, as an arctoid lineage becomes more aquatic it tends to increase its body mass and this may have an effect on its bone microstructure. Body mass and P are positively correlated and body mass and C are negatively correlated. This indicates that the trend in Arctoidea is towards a decrease in bone compactness as body mass increases. These results suggest that perhaps unlike other aquatic tetrapod groups, swimming arctoids do not tend to have more compact bones and that long bone microstructure may not be a good

predictor of swimming behaviour in arctoids. Further studies of bone microstructure might use non-load bearing elements, such as ribs, to better understand whether changes in bone compactness are associated with aquaticism in arctoids.

Bone Compactness in *Puijila*

Is there evidence for increased bone density in fossil pinnipeds? *Puijila* has a larger body mass and thicker cortical bone than the average for all terrestrial arctoids in this study. Body mass estimates for *Puijila* are closer to the average size of semi-aquatic arctoids. The humerus and femur of *Puijila* have lower values of P than semi-aquatic arctoids, but higher values than otariids and walrus. The more distal long bones have lower values of P than the average of any behavioural group. Therefore, its lower values of P which correspond to higher bone compactness may indicate compactness in this transitional fossil which is higher than expected. However, these results are taken solely from CT scan data and were not confirmed with natural breaks in the specimen. The resolution of the CT scans and the possibility of matrix infilling the medullary cavity could have artificially increased the compactness values for the long bones of *Puijila*.

Puijila was consistently predicted as a semi-aquatic or aquatic arctoid using DFA when bone microstructure variables and body mass data from the modern arctoids were used as covariates. However, when $\log(m_b)$ was removed from the analysis the overall predictive accuracy of the DFA usually decreased, though *Puijila* was still classified as a swimming arctoid. This is another indication that body mass is an important predictor of swimming behaviour in this mammal group. In the absence of body mass, removal of P_t

from DFA (n=43) caused *Puijila* to be misclassified as terrestrial in most analyses indicating it may also be important to the classification of *Puijila* as a swimming arctoid. No one variable appeared to be driving the classification of *Puijila* in analyses involving C, S and Min (n=27). With or without the inclusion of body mass, *Puijila* was consistently classified as a swimming arctoid no matter which variable was removed.

Implications for Other Aquatic Mammal Groups

If body size plays such an important role in the microstructure of arctoid long bones, it is likely that changes in bone compactness in early pinniped evolution would have resulted only from correlated evolution between bone compactness and body mass. How does this affect the other groups which have been suggested to exhibit increased bone compactness for buoyancy control in their semi-aquatic fossil ancestors?

The land-to-sea evolution of sirenians is captured by the quadrupedal and semi-aquatic fossil, *Pezosiren portelli*, and in cetaceans by transitional forms such as *Indohyus*, pakicetids and ambulocetids (Thewissen and Fish, 1997; Domning, 2001; Thewissen and Williams, 2002). Increased bone compactness in sirenians is found mostly in the ribs and is present in the quadrupedal form *Pezosiren portelli* (Domning, 2001). The specialization persists even in their modern fully aquatic forms, and has been shown by Domning and Debuffrenil (1991) to provide ballast and keep the animal parallel to the substrate while feeding. Therefore, there is good evidence that this specialization is related to their swimming behaviour and feeding and not to their large body mass.

It has been suggested that early cetaceans show evidence of increased cortical

bone thickness for buoyancy control during their evolution. Instead of thick cortical bone, modern cetaceans use trabecular struts to strengthen their bones and brace them against the physical stresses created during swimming (Madar, 1998; Gray et al., 2007)). Within ancestral cetaceans, which have been suggested to display increased bone density, there is also an increase in body size from the more terrestrial ancestors of cetaceans, such as *Indohyus*, to the more aquatic ancestral cetaceans such as baileosaurids. Based on a survey of modern artiodactyls that found their average cortical bone thickness ratio to be between 0.65 and 0.7, *Indohyus* was interpreted to be semi-aquatic as it had a smaller ratio of 0.42 (Thewissen et al., 2007). The earliest semi-aquatic pakicetids and ambulocetids were still able to walk on land (Thewissen and Williams, 2002). Some pakicetid long bones have no medullary canal, being completely filled in with compact bone (Thewissen and Williams, 2002). There is evidence for systematic increases in bone density in ambulocetids as well (Gray et al., 2007; Madar, 2007). Therefore, although there is an increase in body size in ancestral cetaceans, there is evidence for increases in bone density that may not be explained by body mass increases alone.

SUMMARY

This study shows there is evidence in Arctoidea for correlated evolution between swimming behaviour and body mass and certain aspects of bone microstructure. Body mass is an important predictor of swimming behaviour within Arctoidea. Bone microstructure does not appear to be an effective predictor of swimming behaviour in

arctoids when the influence of body mass is removed from the data. Arctoids tend to have reduced bone compactness as their body size increases, which is contrary to the observations of previous studies. Discriminant function analyses support the predictions made from the musculoskeletal specializations of *Puijila* that it was semi-aquatic. *Puijila* has a higher estimated body mass and more compact long bones than the average values for terrestrial arctoids. Its body mass estimates are most similar in size to the average of semi-aquatic arctoids, but its distal bones are more compact than semi-aquatic arctoids. Although there is evidence to support that increase in bone compactness is an aquatic specialization in some mammal lineages, it does not appear to be the case for Arctoidea. More taxonomically specific investigations of other marine tetrapod lineages could determine whether increased bone compactness is truly correlated with swimming behaviour in other aquatic amniotes, independent of the influences of body size.

CONCLUSION

The specializations of the forelimb of *Puijila* suggest that it was adapted to provide powerful movements and was likely used more frequently during swimming, than the forelimb of *Lontra*. *Puijila* appears to have a more specialized forelimb than modern lutrines, yet less specialized than its fossil relative *Potamotherium*. The long bones of *Puijila* appear to have higher compactness than those of terrestrial arctoids, possibly indicating their bone microstructure reflected a specialization for aquaticism.

Discriminant function analyses based on bone microstructure variables and body mass of modern arctoids predict *Puijila* was a semi-aquatic arctoid, which supports the fossil musculoskeletal evidence. In arctoids, there is a positive correlation between body mass and swimming behaviour and evidence for correlated evolution between bone microstructure and body mass. Results of phylogenetically independent contrasts analyses indicate that bone microstructure data is not as informative about an arctoid's swimming behaviour as it likely is for other aquatic mammal groups.

Examination of more fossil stem pinnipeds could provide further insight into the larger patterns of bone compactness in ancestral pinnipeds. This understanding of bone compactness in other ancestral pinnipeds would build on the evidence provided in this study from the comparative description of the forelimb of *Puijila* and the examination of bone compactness in arctoids, to shed further light on the early evolution of Pinnipedia.

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APPENDIX 1

SUMMARY OF IMPORTANT RECONSTRUCTED MUSCULATURE, THEIR VISIBLE POINTS OF
ORIGIN AND INSERTION AND THEIR PROPOSED FUNCTION,
IN THE FORELIMB OF *PUIJILA DARWINI*

Muscle(s)	Origin	Insertion	Specialization	Proposed Function
Teres major	"Teres fossa", also known as area of posterodorsal expansion of the caudal angle of the scapula	On medial side of the humerus, near the midpoint of the shaft (presumed)	Enlargement is indicated by the development of a large expansion of the caudal angle creating an incipient "teres fossa"	Flexion of shoulder joint Adduction of the humerus Possibly internal rotation of the humerus
Biceps	Coracoid process of the scapula (presumed)	Biceps tubercle of the radius	Evidence for enlargement in the deep bicipital groove of the humerus and large biceps tubercle of the radius	Flexion of the elbow joint Extension of the shoulder joint
Triceps	Infraglenoid tubercle on the caudal border of the scapula (long head), on the lateral side of the shaft of the humerus just inferior to the infraspinatus fossa of the humerus and greater tuberosity (lateral) (presumed) posterior to the lesser tuberosity of the humerus (medial) (presumed)	olecranon	Enlargement of the muscle group indicated by an enlarged olecranon and infraglenoid tubercle (long head) on the caudal border of the scapula.	Extension of the elbow

Muscle(s)	Origin	Insertion	Specialization	Proposed Function
Brachialis	Majority of the lateral side of the humerus, extending from the lateral triceps scar, possibly ending at or near lateral epicondylar wing (presumed)	Into a triangular groove just distad of the trochlear notch of the ulna	Deep groove for the insertion on the ulna indicates the likely enlargement of this muscle	Flexion of the elbow joint
Deltoid	Acromion/Metacromion, Scapular spine, possibly extending to the dorsal margin of the Infraspinatus fossa and partially to the "teres fossa"	The lateral part deltopectoral crest of the humerus	Enlargement of this muscle and specializations of the scapula indicate that is may have shared similarities to that of pinnipeds	Flexion of the shoulder joint Abduction of the humerus Possibly external rotation of the humerus
Supraspinatus	Supraspinatus fossa of the scapula	Greater tuberosity of the humerus	Presumed enlarged based on the size of the greater tuberosity	Abduction of the humerus Extension of the shoulder joint
Infraspinatus	Infraspinatus fossa of the scapula	Infraspinatus fossa of the humerus, on the lateral facing side of the greater tuberosity	Reduced in size in proportion to supraspinatus. Depth of fossa may indicate strengthening of the muscle.	Abduction of the humerus External rotation of the humerus
Subscapularis	Medial side of the scapula	Lesser tuberosity of the humerus	Presumed enlarged based on the size of the scapula and lesser tuberosity of the humerus	Adduction of humerus Extension and flexion of shoulder joint Possibly internal rotation of the humerus

Muscle(s)	Origin	Insertion	Specialization	Proposed Function
Pectoralis	Sternum and trunk (presumed)	Medial part of the deltopectoral crest of the humerus	Enlarge and raised deltopectoral crest indicates enlargement of this muscle group	Adduction of humerus Flexion and extension of shoulder joint
Anaconeus	Olecranon (lateral, medial)	Posterior side of the lateral epicondylar wing of the humerus (lateral), posterior surface of the medial epicondyle (medial) A deep depression spanning the distal half of the medial side of the radius	Large lateral epicondylar wing indicates enlargement of this muscle group.	Assists with extension of the elbow Possibly stabilization of elbow joint
Pronator quadrate	A shelf of bone spanning the distal 1/3 of the medial side of the ulna			Pronation of forearm

APPENDIX 2

LIST OF *POTAMOTHERIUM* MATERIAL AT THE CANADIAN MUSEUM OF NATURE,
OTTAWA, CANADA

Element	Specimen Number	Notes
Humerus	CMNFV-54090	left, complete
Ulna	CMNFV- 54091	Right, complete, weathered
Ulna	CMNFV - 54092	Right, partial, lacks distal ¼ of shaft
Radius	CMNFV - 54093	Left, complete
Radius	CMNFV - 54094	Right, complete
Femur	CMNFV - 54095	Left, complete
Tibia	CMNFV - 54096	Right, complete
Partial Pelvis	CMNFV - 54097	Left illium and ½ acetabulum
Partial Pelvis	CMNFV - 54098	Left acetabulum and partial ischium
Calcaneum	CMNFV - 54099	Right, complete
Proximal Phalanx	CMNFV – 54100	Unknown, compete
Proximal Phalanx	CMNFV – 54101	Unknown, compete
Proximal Phalanx	CMNFV – 54102	Unknown, compete
Proximal Phalanx	CMNFV – 54103	Unknown, compete
Intermediate Phalanx	CMNFV -54104	Unknown, compete

APPENDIX 3

LIST OF SPECIES, WITH SPECIMEN NUMBERS, CT SCANNED AND X-RAY IMAGED AT THE
SMITHSONIAN NATIONAL MUSEUM OF NATURAL HISTORY

USNM #	Species name	Common Name	Gender
259027	<i>Ailuropoda melanoleuca</i>	Giant Panda	male
305771	<i>Ailurus fulgens</i>	Red panda	male
155324	<i>Aonyx cinereus</i>	Oriental small-clawed otter	male
A23331	<i>Arctocephalus australis</i>	South American Fur Seal	male
396921	<i>Arctocephalus forsteri</i>	New Zealand Fur	male
258588	<i>Callorhinus ursinus</i>	Northern Fur Seal	male
550317	<i>Cystophora cristata</i>	Hooded Seal	male
A21336	<i>Enhydra lutris</i>	Sea otter	male
500251	<i>Erignathus barbatus</i>	Bearded Seal	male
A7141	<i>Eumetopias jubatus</i>	Northern Sea Lion	male
272316	<i>Gulo gulo</i>	Wolverine	male
446405	<i>Halichoerus grypus</i>	Grey Seal	male
550358	<i>Hydrurga leptonyx</i>	Leopard Seal	male
504875	<i>Leptonychotes weddellii</i>	Weddell Seal	Unknown
256976	<i>Lontra canadensis</i>	River otter	male
512791	<i>Lontra felina</i>	Marine otter	female
255133	<i>Lontra longicaudis</i>	Neotropical otter	male
505316	<i>Martes americana</i>	American marten	male
173316	<i>Martes flavigula</i>	Yellow-throated marten	male
319224	<i>Martes foina</i>	Beech marten	male
188221	<i>Martes pennanti</i>	Fisher	male
296107	<i>Mellivora capensis</i>	Honey Badger	male
564278	<i>Mephitis mephitis</i>	Striped skunk	male
219058	<i>Mirounga angustirostris</i>	Northern Elephant Seal	male
219059	<i>Monachus monachus</i>	Mediterranean Monk Seal	Unknown
546171	<i>Mustela ermina</i>	Ermine	male
A35088	<i>Mustela frenata</i>	Long-tailed weasel	male
233978	<i>Mustela nivalis</i>	Least weasel	male
257966	<i>Mustela putorius</i>	European polecat	male
239584	<i>Mustela sibirica</i>	Siberian weasel	male
134019	<i>Mustela vison</i>	American mink	male
504729	<i>Neophoca cinerea</i>	Australian Sea Lion	male
A07139	<i>Odobenus rosmarus</i>	Walrus	male
484912	<i>Otaria flavescens</i>	South American Sealion	male
504298	<i>Phoca vitulina</i>	Harbor Seal	male
396274	<i>Procyon lotor</i>	Raccoon	male
304663	<i>Pteronura brasiliensis</i>	Giant Otter	male
564281	<i>Spilogale putorius</i>	Western spotted skunk	male
264140	<i>Taxidea taxus</i>	American badger	male
303193	<i>Ursus americanus</i>	Black Bear	male
265076	<i>Ursus arctos</i>	Brown Bear	male
260231	<i>Ursus martimus</i>	Polar Bear	male
200847	<i>Zalophus californianus</i>	California Sea Lion	male

APPENDIX 4

RAW DATA FROM ALL LONG BONES COLLECTED FROM CT SCANS, USING BONE PROFILER

V.4.11.11 (FOR WINDOWS), AND FROM X-RAY IMAGES

Species Name	SC	log(m _b)	P _h	P _r	P _u	P _{fe}	P _t	P _{fi}
<i>Ailuropoda melanoleuca</i>	0	2.07	0.5973380	0.5050580	0.4551983	0.4963829	0.4594226	0.4005746
<i>Ailurus fulgens</i>	0	0.65	0.5498242	0.3953088	0.4354320	0.5181319	0.3797437	0.1836763
<i>Aonyx cinereus</i>	2.25	0.54	0.4059933	0.2613576	0.2313812	0.5090389	0.3770441	0.2755503
<i>Arctocephalus australis</i>	3	2.24	0.2911528	0.5216103	0.2863445	0.4289002	0.4193113	0.2065515
<i>Arctocephalus forsteri</i>	3	2.01	0.2920797	0.2355175	0.4306320	0.4847026	0.4999878	0.4928960
<i>Callorhinus ursinus</i>	3.5	2.36	0.3237413	0.4589362	0.3765924	0.2569423	0.4921991	0.3464017
<i>Cystophora cristata</i>	4	2.48	0.8552613	0.8036550	0.7722441	0.9018047	0.7202737	0.7945282
<i>Enhydra lutris</i>	3	1.53	0.4076511	0.1755594	0.2018794	0.5856538	0.2606014	0.0000000
<i>Erignathus barbatus</i>	3.5	2.45	0.5469963	0.5653588	0.5138950	0.6120743	0.5284751	0.5745754
<i>Eumetopias jubatus</i>	3.5	3.00	0.4276342	0.7133160	0.3565546	0.4068707	0.4645630	0.3496610
<i>Gulo gulo</i>	0	1.29	0.6606291	0.4787370	0.3812490	0.5477382	0.4593659	0.2726465
<i>Halichoerus grypus</i>	3.25	2.38	0.5637015	0.6250275	0.5404518	0.6520446	0.5698276	0.5094555
<i>Hydrurga leptonyx</i>	3.33	2.43	0.4371081	0.4940154	0.4607671	0.7560920	0.4595965	0.5334154
<i>Leptonychotes weddellii</i>	3.5	2.63	0.6145437	0.6535131	0.5957941	0.7280679	0.0464971	0.4640370
<i>Lontra canadensis</i>	2.25	1.08*	0.5784453	0.4411083	0.3633829	0.5857539	0.4207534	0.1369529
<i>Lontra felina</i>	2.5	0.65*	0.4456650	0.4608465	0.3794341	0.5323569	0.3232095	0.2022557
<i>Lontra longicaudis</i>	2.25	1.1*	0.4507286	0.3283233	0.2641402	0.5578199	0.3052416	0.0725806
<i>Martes americana</i>	0	-0.05	0.5291442	0.4214804	0.3252165	0.6449945	0.4041659	0.0622605
<i>Martes flavigula</i>	0	0.40	0.5660142	0.4465850	0.3507179	0.5876628	0.5128427	0.2839338
<i>Martes foina</i>	0	0.23	0.5477397	0.3513528	0.3396408	0.5337876	0.4637902	0.2132877
<i>Martes pennanti</i>	0	0.61	0.5864000	0.4084748	0.4152788	0.6003103	0.4125214	0.2461470
<i>Mellivora capensis</i>	0	1.00	0.4678190	0.3294832	0.4267088	0.4733655	0.3762604	0.1236637
<i>Mephitis mephitis</i>	0	0.13	0.5623414	0.4671320	0.2914332	0.5398643	0.4064490	0.1390475
<i>Mirounga angustirostris</i>	4	3.37	0.8260646	0.7788179	0.8226374	0.9433604	0.7840720	0.8013254
<i>Monachus monachus</i>	3.25	2.44	0.4276220	0.5452092	0.4446208	0.7329293	0.6920841	0.4405488
<i>Mustela ermina</i>	0	-0.69	0.6000892	0.5738686	0.4369753	0.6512887	0.6065098	0.3132033

Species Name	SC	log(m _b)	P _h	P _r	P _u	P _{fe}	P _t	P _{fi}
<i>Mustela frenata</i>	0	-0.85	0.4543812	0.2763082	0.2818923	0.5923790	0.4783425	0.2418735
<i>Mustela nivalis</i>	0	-0.86	0.4142382	0.3421420	0.2518005	0.4989608	0.3542262	0.0000000
<i>Mustela putorius</i>	0.25	-0.10	0.4606136	0.4464129	0.3742625	0.4896087	0.4002562	0.1725780
<i>Mustela sibirica</i>	0.25	-0.13	0.5514643	0.3686193	0.3259698	0.5692360	0.3967162	0.0174755
<i>Neophoca cinerea</i>	3	2.48	0.2562585	0.3561949	0.3045766	0.2796337	0.2799056	0.2096598
<i>Neovision vison</i>	1.25	0.17	0.5306543	0.3944434	0.3773509	0.5800509	0.4058563	0.1141787
<i>Odobenus rosamarus</i>	3	3.10	0.2854668	0.6654243	0.5621513	0.5494597	0.3799108	0.3745756
<i>Otaria flavescens</i>	3	2.44	0.5042385	0.4580815	0.2865767	0.3950767	0.4895091	0.3620703
<i>Phoca vitulina</i>	3.5	2.08	0.5318804	0.7045352	0.2864088	0.6922249	0.4383983	0.5237789
<i>Procyon lotor</i>	0.25	0.83	0.6247855	0.3412021	0.3492610	0.5822910	0.4894879	0.2120685
<i>Pteronura brasiliensis</i>	2.25	1.48	0.6033320	0.5852848	0.5467044	0.6336903	0.5719009	0.4807296
<i>Spilogale putorius</i>	0	-0.22	0.5697086	0.4147451	0.2705372	0.5203625	0.3926928	0.1815872
<i>Taxidea taxus</i>	0	0.90	0.6466950	0.4322030	0.3504547	0.5839600	0.5580314	0.2885262
<i>Ursus americanus</i>	0	2.28	0.6650842	0.5101778	0.5458777	0.5747143	0.5745977	0.4051585
<i>Ursus arctos</i>	0	2.33	0.5281771	0.3660740	0.2824641	0.4085901	0.3445152	0.1722185
<i>Ursus martimus</i>	1.5	2.66	0.7004435	0.5983786	0.5005060	0.5053378	0.5487914	0.4833556
<i>Zalophus californianus</i>	3.25	2.48	0.4625298	0.6732024	0.5080019	0.5406730	0.5092627	0.3931928

*represents body mass estimates which were altered from Walker's Mammal of the World using Animal Diversity Web. Where ever possible, body mass estimates were confirmed with Silva and Downing (1995).

Name	S _h	S _r	S _u	S _{fe}	S _t	S _{fi}
<i>Ailuropoda melanoleuca</i>	0.0166424	0.0230684	0.0236231	0.0121455	0.0245829	0.0260315
<i>Arctocephalus australis</i>	0.0541709	0.0582418	0.0404148	0.0520851	0.0461309	0.0510158
<i>Arctocephalus forsteri</i>	0.0518578	0.0619361	0.0231455	0.0562028	0.0299843	0.0467583
<i>Callorhinus ursinus</i>	0.0424910	0.0464808	0.0312928	0.0320800	0.0015433	0.0214332
<i>Cystophora cristata</i>	0.0214319	0.0530270	0.0342081	0.0145582	0.0633835	0.0155484

Name	S _h	S _r	S _u	S _{fe}	S _t	S _{fi}
<i>Enhydra lutris</i>	0.0462206	0.0339050	0.0353384	0.0342946	0.0341329	0.0000000
<i>Erignathus barbatus</i>	0.0515568	0.0560804	0.0625094	0.0756683	0.0877279	0.0285441
<i>Eumetopias jubatus</i>	0.0751858	0.0676959	0.0468197	0.0582334	0.0253762	0.0374393
<i>Gulo gulo</i>	0.0254875	0.0301598	0.0211599	0.0081858	0.0316597	0.0210318
<i>Halichoerus grypus</i>	0.0522953	0.0499036	0.0348020	0.0422330	0.0761502	0.0321067
<i>Hydrurga leptonyx</i>	0.0490034	0.0398103	0.0784898	0.0222748	0.0528107	0.0594968
<i>Leptonychotes weddellii</i>	0.0535569	0.0294574	0.0665434	0.0331909	0.0947428	0.0491733
<i>Lontra canadensis</i>	0.0417500	0.0460868	0.0258425	0.0184767	0.0211474	0.0096919
<i>Lontra longicaudis</i>	0.0171750	0.0310756	0.0114462	0.0145410	0.0159274	0.0000000
<i>Mellivora capensis</i>	0.0214440	0.0390799	0.0266995	0.0168835	0.0215993	0.0201016
<i>Mirounga angustirostris</i>	0.0513940	0.0726249	0.0462913	0.0144788	0.0620418	0.0387832
<i>Monachus monachus</i>	0.0520033	0.0590427	0.0496031	0.0319361	0.0440194	0.0571727
<i>Neophoca cinerea</i>	0.0730226	0.0848570	0.0696766	0.0600149	0.0509825	0.0503563
<i>Odobenus rosmarus</i>	0.0392949	0.0869702	0.0804101	0.0796548	0.0769899	0.0328543
<i>Otaria flavescens</i>	0.0580111	0.0786940	0.0403112	0.0511408	0.0496834	0.0546303
<i>Phoca vitulina</i>	0.0528515	0.0515826	0.0403728	0.0408960	0.0671909	0.0727714
<i>Pteronura brasiliensis</i>	0.0434117	0.0405901	0.0238577	0.0218351	0.0251105	0.0761205
<i>Taxidea taxus</i>	0.0235870	0.0383947	0.0337576	0.0141398	0.0254251	0.0000000
<i>Ursus Americanus</i>	0.0251232	0.0535473	0.0392158	0.0099972	0.0286800	0.0171073
<i>Ursus arctos</i>	0.0218892	0.0403623	0.0423454	0.0200312	0.0354189	0.0307344
<i>Ursus martimus</i>	0.0377659	0.0598112	0.0558947	0.0339420	0.0540435	0.0362697
<i>Zalophus californianus</i>	0.0581053	0.0558125	0.0373502	0.0426764	0.0294299	0.0319615

Name	C _h	C _r	C _u	C _{fe}	C _t	C _{fi}
<i>Ailuropoda melanoleuca</i>	0.638	0.737	0.789	0.749	0.791	0.834
<i>Gulo gulo</i>	0.562	0.766	0.851	0.696	0.781	0.926
<i>Mellivora capensis</i>	0.779	0.886	0.812	0.772	0.856	0.984
<i>Taxidea taxus</i>	0.571	0.804	0.872	0.656	0.685	1.000
<i>Ursus americanus</i>	0.547	0.727	0.690	0.661	0.662	0.832
<i>Ursus arctos</i>	0.716	0.860	0.913	0.827	0.876	0.967
<i>Ursus martimus</i>	0.501	0.622	0.736	0.736	0.686	0.760
<i>Lontra canadensis</i>	0.655	0.794	0.862	0.653	0.820	0.966
<i>Lontra longicaudis</i>	0.794	0.887	0.929	0.680	0.906	1.000
<i>Pteronura brasiliensis</i>	0.626	0.651	0.695	0.591	0.670	0.749
<i>Arctocephalus australis</i>	0.899	0.713	0.944	0.805	0.829	0.947
<i>Arctocephalus forsteri</i>	0.904	0.931	0.823	0.749	0.743	0.755
<i>Enhydra lutris</i>	0.825	0.966	0.955	0.649	0.939	1.000
<i>Neophoca cinerea</i>	0.914	0.854	0.903	0.909	0.911	0.948
<i>Odobenus rosmarus</i>	0.937	0.627	0.712	0.697	0.914	0.895
<i>Otaria flavescens</i>	0.763	0.784	0.944	0.827	0.776	0.892
<i>Halichoerus grypus</i>	0.704	0.599	0.709	0.565	0.654	0.776
<i>Monachus monachus</i>	0.812	0.663	0.792	0.455	0.512	0.812
<i>Zalophus californianus</i>	0.801	0.533	0.740	0.696	0.740	0.843
<i>Hydrurga leptonyx</i>	0.799	0.750	0.768	0.424	0.779	0.698
<i>Callorhinus ursinus</i>	0.888	0.789	0.854	0.929	0.751	0.882
<i>Erignathus barbatus</i>	0.697	0.676	0.722	0.603	0.720	0.753
<i>Eumetopias jubatus</i>	0.795	0.475	0.880	0.821	0.789	0.873
<i>Leptonychotes weddellii</i>	0.655	0.534	0.630	0.460	0.749	0.771
<i>Phoca vitulina</i>	0.743	0.495	0.944	0.514	0.833	0.708
<i>Cystophora cristata</i>	0.322	0.354	0.401	0.187	0.469	0.376
<i>Mirounga angustirostris</i>	0.325	0.381	0.316	0.116	0.372	0.349

Name	Min _h	Min _r	Min _u	Min _{te}	Min _t	Min _{fi}
<i>Ailuropoda melanoleuca</i>	0.0000369	0.0000004	0.0000003	0.0000005	0.0435893	0.0000007
<i>Arctocephalus australis</i>	0.0000008	0.0000003	0.3694005	0.0000007	0.0692192	0.0000012
<i>Arctocephalus forsteri</i>	0.0000013	0.0000007	0.0689025	0.0000004	0.0000007	0.0000003
<i>Callorhinus ursinus</i>	0.0000012	0.0418204	0.0087951	0.0000007	0.0015433	0.0000007
<i>Cystophora cristata</i>	0.0767542	0.0000001	0.0000001	0.0024922	0.0000003	0.0000001
<i>Enhydra lutris</i>	0.0000007	0.0000013	0.0000013	0.0000004	0.1758469	1.0000000
<i>Erignathus barbatus</i>	0.0395623	0.0265505	0.0062696	0.0017025	0.0897002	0.2656494
<i>Eumetopias jubatus</i>	0.0000007	0.0000001	0.1253067	0.0079647	0.0432842	0.0000008
<i>Gulo gulo</i>	0.0114409	0.0000007	0.0000004	0.0000001	0.0000007	0.0000007
<i>Halichoerus grypus</i>	0.0996780	0.0068226	0.0220958	0.0000002	0.0000010	0.1423305
<i>Hydrurga leptonyx</i>	0.0000012	0.0145790	0.0000003	0.0005874	0.0065722	0.0000004
<i>Leptonychotes weddellii</i>	0.1220952	0.0065982	0.0000004	0.0000000	0.0000004	0.0000007
<i>Lontra canadensis</i>	0.0000003	0.0000008	0.0000012	0.0000004	0.0000007	0.0000010
<i>Lontra longicaudis</i>	0.0000004	0.0000013	0.0000008	0.0000004	0.0000006	1.0000000
<i>Mellivora capensis</i>	0.0000004	0.0000010	0.0000007	0.0000003	0.0000008	0.0000023
<i>Mirounga angustirostris</i>	0.0233824	0.0000001	0.0000001	0.0055687	0.0000001	0.0000001
<i>Monachus monachus</i>	0.0334517	0.0024249	0.0000006	0.0000001	0.0004134	0.0803218
<i>Neophoca cinerea</i>	0.0771293	0.0330856	0.1255401	0.0000009	0.0000013	0.0000007
<i>Odobenus rosmarus</i>	0.2844950	0.2016132	0.1608710	0.0668829	0.4815634	0.2737260
<i>Otaria flavescens</i>	0.1233817	0.0665030	0.3703900	0.0078636	0.1101806	0.2812033
<i>Phoca vitulina</i>	0.1331817	0.0009838	0.3696452	0.0000002	0.1939267	0.0000006
<i>Pteronura brasiliensis</i>	0.0000002	0.0000004	0.0000003	0.0000004	0.0000004	0.0000002
<i>Taxidea taxus</i>	0.0000003	0.0000006	0.0000012	0.0000004	0.0000007	1.0000000
<i>Ursus americanus</i>	0.0000003	0.0000002	0.0087157	0.0000000	0.0000007	0.0000004
<i>Ursus arctos</i>	0.0000003	0.0000007	0.0000010	0.0000004	0.0000012	0.0000023
<i>Ursus martimus</i>	0.0000001	0.0000001	0.0000004	0.0000003	0.0000008	0.0000068
<i>Zalophus californianus</i>	0.1273200	0.0000002	0.0133210	0.0022533	0.0172148	0.0000045

APPENDIX 5

RUBRIC USED FOR CALCULATING SWIMMING CATEGORY

	0	1	2	3	4
External Modifications	None	Are not significant, may have webbed feet, but limb proportions still appear terrestrial and body not obviously fusiform	Slight modifications. Will have webbed feet, a slightly more fusiform body and may be clumsy on land	Display distinct aquatic modifications such as large paddle-like feet or flippers, a fusiform body and are clumsy on land	Extreme modifications for aquaticism, such as a fusiform body and flippers, which may include soft tissue adaptations. Adaptations extreme enough to severely limit locomotion on land.
Habitat	None	Spends a portion of daily life in the water, though still more time on land than in water. May use water to escape predation. Habitat is predominantly onshore, or tied closely to shore	Spends equal, or slightly more, time in the water than on land. Uses water to escape predation. Habitat is dependent on both land and water.	Spends most or all of daily life in the water, will spend more time in water than on land. Aquatic habitat is close to shore, yet may or may not need to return to shore daily. Will not venture too far from shore for long periods	Spends most or all of daily life in the water, will spend more time in water than on land. Aquatic habitat can be near shore, but may leave to be at sea for days or months (pelagic).
Food Source	Forage almost exclusively on land	Foraging on both land and in water	Forage dependant on water, but can forage on land as well.	Forage exclusively in water (near shore or benthic organisms)	Forage exclusively in water (near shore, benthic or pelagic organisms)
Diving	May swim, but does not actively seek out water to swim	Swims but does not dive deeply, often, or for long periods.	Dives 0-1min, or 0-10m	Dives 1-10min or 10-100m	dives last >10min and depths >100m

APPENDIX 6

VARIABLE NAMES AND DEFINITIONS

Symbol	Variable Name	Definition
$\log(m_b)$	Log Body Mass	Log of the average body mass for the males of a species.
SC	Swimming Behavior Category	A number between 0 and 4 which represents a species overall swimming behavior.
$P_{h,r,u,fe,t,fi}$	Cortical bone thickness	Value produced from Bone Profiler. Equivalent to K ratio ($K=ID/ED$). The subscript indicates which bone the value corresponds to.
P_{for}		Average of the values of P for the forelimb bones, for a species. $AVG(P_h+P_r+P_u)$
P_{hind}		Average of the values of P for the hind limb bones, for a species. $AVG(P_{fe}+P_t+P_{fi})$
P_{avg}		Average of the values of P for the all six bones, for a species. $AVG(P_h+P_r+P_u+P_{fe}+P_t+P_{fi})$
$S_{h,r,u,fe,t,fi,for,hind,avg}$	Transition zone	Represents the width of the transition zone between medullary cavity and cortical bone. The subscript indicates which bone the value corresponds to.
$C_{h,r,u,fe,t,fi,for,hind,avg}$	Overall bone compactness	The total number of bone pixels over the total number of pixels in the section. The subscript indicates which bone the value corresponds to.
$Min_{h,r,u,fe,t,fi,for,hind,avg}$	Minimum compactness	Reflects the number and thickness of trabeculae in the medullary cavity. The subscript indicates which bone the value corresponds to.

APPENDIX 7**INSTRUCTIONS ON HOW TO CALCULATE K-STATISTIC IN R USING NEXUS FILES CREATED FROM MESQUITE**

1. Create a nexus file of your tree in Mesquite (the order of the taxa in the nexus file must follow the order of the taxa in the text file of characters you created. It is easiest to alphabetize the taxa in the taxa block in mesquite and your excel file)
 - a. Select a branch length algorithm from the “Tree” menu
 - b. “Tree” menu -> “Store Tree”, then “File” menu-> “Export”... and choose “Export Nexus file” (the first option) and hit OK, then choose your “Tree Block” and hit OK and then check off the box “Include Taxa Block” and hit OK. Give your nexus file a name and “Save”.
2. Create a .txt file by choosing “Save as...” in excel and choosing “Text (tab delimited)” from the “Save as type:” options. Make a separate .txt file for **all** your continuous characters. (REMEMBER: The order of the taxa in the Table must match the order of the taxa in the nexus file exactly. This is easiest by alphabetizing them in both Mesquite and Excel. DO NOT INCLUDE TAXA NAMES in you .txt files.)
3. Place both the nexus tree file and the character text files in “My Documents”
4. Install the latest version of R.
5. Open R and Install the following packages: ape, picante, and vegan.

- a. "Packages" menu -> "Install Packages..." -> select your region from the list and hit OK -> select one of the packages you would like to install and hit OK. Repeat if needed for other packages.
6. Load the following packages: ape, picante, vegan (Hint: loading picante first will automatically load the other needed packages)
 - a. "Packages" menu -> "Load Package..." -> select one of the packages you would like to load and hit OK. Repeat if need for other packages.
7. To open and view the nexus file in R type **read.nexus("nameofyourfile")** into the command line and hit enter.
8. To assign the tree to the variable "phy" type **Phy<-read.nexus("nameofyourfile")** into the command line and hit enter.
9. Then to open and view a .txt character file in R type **read.table("nameofyourfile.txt")** into the command line and hit enter.
10. Then assign the character values to "x" by typing **x<-read.table("nameofyourfile.txt")** into the command line and hitting enter.
11. To calculate K-statistic enter **Kcalc(x,phy)** into the command line and hit enter.
12. Repeat steps 9- 11 for all your characters.
 - a. If you wish to calculate the K-Statistic for your characters using a different branch length algorithm, repeat step 7-8 to open the new nexus file and assign it to "phy" and then repeat steps 9-12 to calculate K-statistic for your characters. (Hint: once you have opened a nexus or .txt file in R, by

using the commands from steps 7 and 9, they remain available and can be used in the calculation by simply reassigning their values to either “phy” or “x” by using steps 8 or 10)

APPENDIX 8

DISCRIMINANT FUNCTION ANALYSIS RESULTS CALCULATED IN JMP

Legend:

□ = Terrestrial (SC=1) ◆ = Semi-aquatic (SC=2) ● = Aquatic (SC=3)
 X = Semi-Pelagic (SC=4) * = *Puijila darwini*

43 Taxa Analyses

Row	Species name:
1	<i>Ailuropoda melanoleuca</i>
2	<i>Ailurus fulgens</i>
3	<i>Aonyx cinereus</i>
4	<i>Arctocephalus australis</i>
5	<i>Arctocephalus forsteri</i>
6	<i>Callorhinus ursinus</i>
7	<i>Cystophora cristata</i>
8	<i>Enhydra lutris</i>
9	<i>Erignathus barbatus</i>
10	<i>Eumetopias jubatus</i>
11	<i>Gulo gulo</i>
12	<i>Halichoerus grypus</i>
13	<i>Hydrurga leptonyx</i>
14	<i>Leptonychotes weddellii</i>
15	<i>Lontra canadensis</i>
16	<i>Lontra felina</i>
17	<i>Lontra longicaudis</i>
18	<i>Martes americana</i>
19	<i>Martes flavigula</i>
20	<i>Martes foina</i>
21	<i>Martes pennanti</i>
22	<i>Mellivora capensis</i>
23	<i>Mephitis mephitis</i>
24	<i>Mirounga angustirostris</i>
25	<i>Monachus monachus</i>
26	<i>Mustela ermina</i>
27	<i>Mustela frenata</i>
28	<i>Mustela nivalis</i>
29	<i>Mustela putorius</i>
30	<i>Mustela sibirica</i>
31	<i>Neophoca cinerea</i>
32	<i>Neovision vison</i>
33	<i>Odobenus rosmarus</i>
34	<i>Otaria flavescens</i>
35	<i>Phoca vitulina</i>
36	<i>Procyon lotor</i>
37	<i>Pteronura brasiliensis</i>
38	<i>Spilogale putorius</i>
39	<i>Taxidea taxus</i>
40	<i>Ursus americanus</i>
41	<i>Ursus arctos</i>
42	<i>Ursus martimus</i>
43	<i>Zalophus californianus</i>
44	<i>Puijila darwini (must.)</i>
45	<i>Puijila darwini (ursid)</i>
46	<i>Puijila darwini (avg.)</i>

39 Taxa Analyses

Row	Species name:
1	<i>Ailurus fulgens</i>
2	<i>Aonyx cinereus</i>
3	<i>Arctocephalus australis</i>
4	<i>Arctocephalus forsteri</i>
5	<i>Callorhinus ursinus</i>
6	<i>Cystophora cristata</i>
7	<i>Enhydra lutris</i>
8	<i>Erignathus barbatus</i>
9	<i>Eumetopias jubatus</i>
10	<i>Gulo gulo</i>
11	<i>Halichoerus grypus</i>
12	<i>Hydrurga leptonyx</i>
13	<i>Leptonychotes weddellii</i>
14	<i>Lontra canadensis</i>
15	<i>Lontra felina</i>
16	<i>Lontra longicaudis</i>
17	<i>Martes americana</i>
18	<i>Martes flavigula</i>
19	<i>Martes foina</i>
20	<i>Martes pennanti</i>
21	<i>Mellivora capensis</i>
22	<i>Mephitis mephitis</i>
23	<i>Mirounga angustirostris</i>
24	<i>Monachus monachus</i>
25	<i>Mustela ermina</i>
26	<i>Mustela frenata</i>
27	<i>Mustela nivalis</i>
28	<i>Mustela putorius</i>
29	<i>Mustela sibirica</i>
30	<i>Neophoca cinerea</i>
31	<i>Neovision vison</i>
32	<i>Odobenus rosmarus</i>
33	<i>Otaria flavescens</i>
34	<i>Phoca vitulina</i>
35	<i>Procyon lotor</i>
36	<i>Pteronura brasiliensis</i>
37	<i>Spilogale putorius</i>
38	<i>Taxidea taxus</i>
39	<i>Zalophus californianus</i>
40	<i>Puijila darwini (must.)</i>
41	<i>Puijila darwini (ursid)</i>
42	<i>Puijila darwini (avg.)</i>

27 Taxa Analyses

Row	Species name:
1	<i>Ailuropoda melanoleuca</i>
2	<i>Arctocephalus australis</i>
3	<i>Arctocephalus forsteri</i>
4	<i>Callorhinus ursinus</i>
5	<i>Cystophora cristata</i>
6	<i>Enhydra lutris</i>
7	<i>Erignathus barbatus</i>
8	<i>Eumetopias jubatus</i>
9	<i>Gulo gulo</i>
10	<i>Halichoerus grypus</i>
11	<i>Hydrurga leptonyx</i>
12	<i>Leptonychotes weddellii</i>
13	<i>Lontra canadensis</i>
14	<i>Lontra longicaudis</i>
15	<i>Mellivora capensis</i>
16	<i>Mirounga angustirostris</i>
17	<i>Monachus monachus</i>
18	<i>Neophoca cinerea</i>
19	<i>Odobenus rosmarus</i>
20	<i>Otaria flavescens</i>
21	<i>Phoca vitulina</i>
22	<i>Pteronura brasiliensis</i>
23	<i>Taxidea taxus</i>
24	<i>Ursus americanus</i>
25	<i>Ursus arctos</i>
26	<i>Ursus martimus</i>
27	<i>Zalophus californianus</i>
28	<i>Puijila darwini (must.)</i>
29	<i>Puijila darwini (ursid)</i>
30	<i>Puijila darwini (avg.)</i>

ANALYSIS #1:

of Taxa: 43

Y, covariates: $\log(m_b)$, P_h , P_r , P_u , P_{fe} , P_t , P_{fi}

X, categories: SC (1-4)

Canonical Plot **Discriminant Scores**

	Training	Excluded
Number Misclassified	5	0
Percent Misclassified	11.63	0
-2LogLikelihood	25.55	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	6.06390	0.1308	2.034	<div><div style="width: 100%;"></div></div>	* 2	0.8665	
2	1	2.04096	0.9037	0.101	<div><div style="width: 100%;"></div></div>	1	0.9037	
3	2	7.66963	0.9075	0.097	<div><div style="width: 100%;"></div></div>	2	0.9075	
4	3	5.35353	0.9999	0.000	<div><div style="width: 100%;"></div></div>	3	0.9999	
5	3	14.41796	0.9982	0.002	<div><div style="width: 100%;"></div></div>	3	0.9982	
6	3	9.58951	0.9646	0.036	<div><div style="width: 100%;"></div></div>	3	0.9646	
7	4	1.27550	1.0000	0.000	<div><div style="width: 100%;"></div></div>	4	1.0000	
8	3	17.83902	0.2207	1.511	<div><div style="width: 100%;"></div></div>	* 2	0.7699	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
9	3	3.96150	0.9244	0.079		3	0.9244	
10	3	8.08164	0.9997	0.000		3	0.9997	
11	1	2.20820	0.7516	0.286		1	0.7516	2 0.25
12	3	4.86380	0.7690	0.263		3	0.7690	2 0.22
13	3	8.31309	1.0000	0.000		3	1.0000	
14	3	26.31980	0.9442	0.057		3	0.9442	
15	2	3.86911	0.3487	1.054		* 1	0.6513	
16	2	2.79068	0.8173	0.202		2	0.8173	1 0.18
17	2	4.06772	0.9109	0.093		2	0.9109	
18	1	3.48875	0.8725	0.136		1	0.8725	2 0.13
19	1	1.23123	0.7025	0.353		1	0.7025	2 0.30
20	1	0.71400	0.8990	0.106		1	0.8990	2 0.10
21	1	0.81269	0.7983	0.225		1	0.7983	2 0.20
22	1	4.41381	0.7390	0.303		1	0.7390	2 0.26
23	1	1.90305	0.8748	0.134		1	0.8748	2 0.13
24	4	1.27550	1.0000	0.000		4	1.0000	
25	3	12.62158	0.9998	0.000		3	0.9998	
26	1	8.62602	0.9864	0.014		1	0.9864	
27	1	7.13548	0.8337	0.182		1	0.8337	2 0.17
28	1	4.82476	0.9499	0.051		1	0.9499	
29	1	3.35583	0.8607	0.150		1	0.8607	2 0.14
30	1	3.75449	0.9830	0.017		1	0.9830	
31	3	7.54055	0.9988	0.001		3	0.9988	
32	1	1.28064	0.9191	0.084		1	0.9191	
33	3	13.57138	1.0000	0.000		3	1.0000	
34	3	8.52702	0.5588	0.582		3	0.5588	2 0.44
35	3	16.62844	0.9999	0.000		3	0.9999	
36	1	2.63551	0.8880	0.119		1	0.8880	2 0.11
37	2	3.98852	0.7614	0.273		2	0.7614	1 0.23
38	1	3.32611	0.9291	0.074		1	0.9291	
39	1	2.61949	0.8317	0.184		1	0.8317	2 0.17
40	1	7.22762	0.4685	0.758		* 2	0.5261	
41	1	12.01635	0.0508	2.980		* 2	0.9373	
42	2	6.72007	0.8091	0.212		2	0.8091	1 0.19
43	3	4.03558	0.9804	0.020		3	0.9804	
44	?	<i>Puijila darwini</i> (mustelid)				~ - 2	0.8724	3 0.12
45	?	<i>Puijila darwini</i> (ursid)				~ - 3	0.7381	2 0.26
46	?	<i>Puijila darwini</i> (avg.)				~ - 2	0.6151	3 0.38

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #2:

of Taxa: 43

Y, covariates: $\log(m_b)$, $\log(P_h)$, $\log(P_r)$, $\log(P_u)$, $\log(P_{fe})$, $\log(P_t)$, $\log(P_{fi})$ **X, categories:** SC (1-4)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	4	0
Percent Misclassified	9.302	0
-2LogLikelihood	28.95	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	4.51328	0.2653	1.327	<div><div></div></div>	* 2	0.7227	
2	1	1.70505	0.8644	0.146	<div><div></div></div>	1	0.8644	2 0.14
3	2	5.88556	0.8372	0.178	<div><div></div></div>	2	0.8372	1 0.16
4	3	7.23689	0.9999	0.000	<div><div></div></div>	3	0.9999	
5	3	14.32955	0.9366	0.065	<div><div></div></div>	3	0.9366	
6	3	13.67650	0.7988	0.225	<div><div></div></div>	3	0.7988	2 0.19
7	4	0.65223	0.9991	0.001	<div><div></div></div>	4	0.9991	
8	3	24.46813	0.9330	0.069	<div><div></div></div>	3	0.9330	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
9	3	3.77594	0.5719	0.559		3	0.5719	2 0.32
10	3	5.21077	0.9978	0.002		3	0.9978	
11	1	1.67721	0.6094	0.495		1	0.6094	2 0.39
12	3	4.54234	0.5239	0.646		3	0.5239	2 0.23 4 0.24
13	3	4.85122	0.9953	0.005		3	0.9953	
14	3	32.94946	0.9361	0.066		3	0.9361	
15	2	0.44464	0.6100	0.494		2	0.6100	1 0.39
16	2	2.38555	0.6553	0.423		2	0.6553	1 0.33
17	2	3.51162	0.8579	0.153		2	0.8579	
18	1	1.76077	0.6987	0.359		1	0.6987	2 0.30
19	1	0.66851	0.7241	0.323		1	0.7241	2 0.28
20	1	0.93129	0.8809	0.127		1	0.8809	2 0.12
21	1	0.75166	0.7879	0.238		1	0.7879	2 0.21
22	1	3.56738	0.6210	0.476		1	0.6210	2 0.38
23	1	2.31196	0.7922	0.233		1	0.7922	2 0.21
24	4	0.65223	0.9999	0.000		4	0.9999	
25	3	6.47609	0.9951	0.005		3	0.9951	
26	1	7.35327	0.9843	0.016		1	0.9843	
27	1	6.27375	0.9297	0.073		1	0.9297	
28	1	23.03979	0.9386	0.063		1	0.9386	
29	1	2.81888	0.8785	0.130		1	0.8785	2 0.12
30	1	0.83089	0.9063	0.098		1	0.9063	
31	3	9.65284	0.9981	0.002		3	0.9981	
32	1	0.62249	0.8325	0.183		1	0.8325	2 0.17
33	3	14.26779	1.0000	0.000		3	1.0000	
34	3	8.45470	0.2855	1.254		* 2	0.6892	
35	3	11.13521	0.9764	0.024		3	0.9764	
36	1	2.51732	0.7516	0.286		1	0.7516	2 0.25
37	2	3.85758	0.5618	0.577		2	0.5618	1 0.39
38	1	3.53174	0.9159	0.088		1	0.9159	
39	1	1.62797	0.6847	0.379		1	0.6847	2 0.32
40	1	7.14839	0.2399	1.428		* 2	0.6101	4 0.14
41	1	11.69725	0.0562	2.878		* 2	0.8854	
42	2	6.83821	0.7087	0.344		2	0.7087	1 0.22
43	3	2.39608	0.9620	0.039		3	0.9620	
44	?	<i>Puijila darwini</i> (mustelid)				~ - 3	0.9864	
45	?	<i>Puijila darwini</i> (ursid)				~ - 3	0.9992	
46	?	<i>Puijila darwini</i> (avg.)				~ - 3	0.9968	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #3:
of Taxa: 43
Y, covariates: $P_h, P_r, P_u, P_{fe}, P_t, P_{fi}$
X, categories: SC (1-4)

Canonical Plot

Discriminant Scores

		Training	Excluded				
Number Misclassified		7	0				
Percent Misclassified		16.28	0				
-2LogLikelihood		44.04					
Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred) Others
1	1	4.07734	0.2820	1.266	<div><div></div></div>	* 2	0.6958

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
2	1	1.92573	0.7205	0.328		1	0.7205	2 0.28
3	2	7.64776	0.4429	0.814		* 3	0.5252	
4	3	4.89177	0.9920	0.008		3	0.9920	
5	3	14.03268	0.9943	0.006		3	0.9943	
6	3	8.16438	0.9676	0.033		3	0.9676	
7	4	0.40596	1.0000	0.000		4	1.0000	
8	3	17.60540	0.0036	5.632		* 1	0.5046	2 0.49
9	3	3.09287	0.8823	0.125		3	0.8823	2 0.11
10	3	7.79030	0.9879	0.012		3	0.9879	
11	1	1.82052	0.7445	0.295		1	0.7445	2 0.26
12	3	4.13890	0.6191	0.479		3	0.6191	2 0.34
13	3	7.35996	0.9970	0.003		3	0.9970	
14	3	25.54015	0.9046	0.100		3	0.9046	
15	2	3.86894	0.1891	1.666		* 1	0.8108	
16	2	2.27007	0.6174	0.482		2	0.6174	1 0.12 3 0.26
17	2	2.85724	0.5515	0.595		2	0.5515	1 0.44
18	1	3.42510	0.8026	0.220		1	0.8026	2 0.20
19	1	1.23101	0.5048	0.684		1	0.5048	2 0.49
20	1	0.52354	0.6830	0.381		1	0.6830	2 0.32
21	1	0.81250	0.6242	0.471		1	0.6242	2 0.38
22	1	4.04499	0.7273	0.318		1	0.7273	2 0.27
23	1	1.80985	0.6671	0.405		1	0.6671	2 0.33
24	4	0.40596	1.0000	0.000		4	1.0000	
25	3	10.71169	0.9571	0.044		3	0.9571	
26	1	3.99467	0.6501	0.431		1	0.6501	2 0.35
27	1	5.71354	0.2994	1.206		* 2	0.6592	
28	1	3.51931	0.6449	0.439		1	0.6449	2 0.35
29	1	2.31010	0.3986	0.920		* 2	0.5706	
30	1	3.51358	0.9289	0.074		1	0.9289	
31	3	7.54051	0.9834	0.017		3	0.9834	
32	1	1.24209	0.7900	0.236		1	0.7900	2 0.21
33	3	11.91345	0.9998	0.000		3	0.9998	
34	3	8.11135	0.2675	1.319		* 2	0.6379	
35	3	16.53366	0.9986	0.001		3	0.9986	
36	1	2.34612	0.8725	0.136		1	0.8725	2 0.13
37	2	3.66381	0.6700	0.401		2	0.6700	1 0.23
38	1	2.09476	0.5685	0.565		1	0.5685	2 0.43
39	1	2.39106	0.7977	0.226		1	0.7977	2 0.20
40	1	4.76698	0.7437	0.296		1	0.7437	2 0.25
41	1	3.54671	0.5056	0.682		1	0.5056	2 0.49
42	2	6.59606	0.5343	0.627		2	0.5343	1 0.46
43	3	3.74763	0.9230	0.080		3	0.9230	
44	?		<i>Puijila darwini</i>			~ - 2	0.8194	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #4:**# of Taxa:** 43**Y, covariates:** $\log(P_h)$, $\log(P_r)$, $\log(P_u)$, $\log(P_{fe})$, $\log(P_t)$, $\log(P_{fi})$ **X, categories:** SC (1-4)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	15	0
Percent Misclassified	34.88	0
-2LogLikelihood	60.05	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Pred. SC	Prob(Pred)	Others
1	1	1.66072	0.5717	0.559		1	0.5717	2 0.39

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Pred. SC	Prob(Pred)	Others
2	1	1.53777	0.5437	0.609		1	0.5437	2 0.42
3	2	5.88490	0.6216	0.475		2	0.6216	1 0.33
4	3	6.71764	0.9912	0.009		3	0.9912	
5	3	14.16855	0.6697	0.401		3	0.6697	2 0.24
6	3	11.31230	0.8671	0.143		3	0.8671	
7	4	0.07154	0.9980	0.002		4	0.9980	
8	3	23.95225	0.0503	2.991		* 1	0.7013	2 0.25
9	3	3.24413	0.2744	1.293		* 2	0.3965	1 0.29
10	3	4.95047	0.8845	0.123		3	0.8845	
11	1	1.08233	0.6241	0.472		1	0.6241	2 0.37
12	3	3.83813	0.3524	1.043		3	0.3524	1 0.22 2 0.31 4 0.11
13	3	4.40850	0.7952	0.229		3	0.7952	2 0.16
14	3	32.65954	0.7607	0.274		3	0.7607	2 0.20
15	2	0.32643	0.4645	0.767		* 1	0.4958	
16	2	1.69124	0.3286	1.113		* 3	0.5314	1 0.14
17	2	2.77001	0.5809	0.543		2	0.5809	1 0.30 3 0.12
18	1	1.74753	0.3758	0.979		* 2	0.5207	3 0.10
19	1	0.66823	0.4753	0.744		* 2	0.4828	
20	1	0.69114	0.5675	0.567		1	0.5675	2 0.42
21	1	0.74530	0.5343	0.627		1	0.5343	2 0.44
22	1	3.38083	0.4830	0.728		1	0.4830	2 0.44
23	1	2.22771	0.4594	0.778		* 2	0.4964	
24	4	0.07154	0.9992	0.001		4	0.9992	
25	3	5.89686	0.8656	0.144		3	0.8656	2 0.10
26	1	2.36841	0.4245	0.857		* 2	0.4388	3 0.11
27	1	4.59085	0.4242	0.858		* 2	0.5508	
28	1	22.68898	0.2891	1.241		* 3	0.5914	2 0.12
29	1	1.79962	0.2557	1.364		* 2	0.4041	3 0.34
30	1	0.35863	0.5549	0.589		1	0.5549	2 0.42
31	3	9.65283	0.9692	0.031		3	0.9692	
32	1	0.40682	0.4495	0.800		* 2	0.4770	
33	3	11.81649	0.9995	0.001		3	0.9995	
34	3	8.08768	0.0552	2.896		* 1	0.4912	2 0.45
35	3	11.02473	0.5282	0.638		3	0.5282	1 0.10 2 0.37
36	1	2.33912	0.6667	0.405		1	0.6667	2 0.33
37	2	3.66623	0.3425	1.071		* 1	0.3520	3 0.13 4 0.17
38	1	2.68428	0.5118	0.670		1	0.5118	2 0.47
39	1	1.34470	0.6241	0.471		1	0.6241	2 0.37
40	1	3.75510	0.5683	0.565		1	0.5683	2 0.29 4 0.12
41	1	3.38772	0.5730	0.557		1	0.5730	2 0.41
42	2	6.30873	0.2877	1.246		* 1	0.6703	
43	3	2.01347	0.8567	0.155		3	0.8567	
44	?					~ - 2	0.4548	1 0.19 3 0.35

Puijila darwini

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #5:**# of Taxa:** 43**Y, covariates:** $\log(m_b)$, P_h , P_r , P_u , P_{fe} , P_t , P_{fi} **X, categories:** SC (1-3)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	6	0
Percent Misclassified	13.95	0
-2LogLikelihood	29.37	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	6.14156	0.1234	2.092	<div><div></div></div>	* 2	0.8644	
2	1	2.04560	0.8806	0.127	<div><div></div></div>	1	0.8806	2 0.12
3	2	6.27673	0.9010	0.104	<div><div></div></div>	2	0.9010	
4	3	4.93721	0.9980	0.002	<div><div></div></div>	3	0.9980	
5	3	15.03648	0.9956	0.004	<div><div></div></div>	3	0.9956	
6	3	10.08716	0.8154	0.204	<div><div></div></div>	3	0.8154	2 0.18
7	3	11.76624	0.6203	0.478	<div><div></div></div>	3	0.6203	2 0.37
8	3	18.47921	0.0993	2.309	<div><div></div></div>	* 2	0.8770	
9	3	1.89713	0.9748	0.026	<div><div></div></div>	3	0.9748	
10	3	8.40963	0.9981	0.002	<div><div></div></div>	3	0.9981	
11	1	2.16923	0.6868	0.376	<div><div></div></div>	1	0.6868	2 0.31
12	3	1.22909	0.9561	0.045	<div><div></div></div>	3	0.9561	
13	3	8.43665	1.0000	0.000	<div><div></div></div>	3	1.0000	
14	3	25.97880	0.9643	0.036	<div><div></div></div>	3	0.9643	
15	2	3.63047	0.3841	0.957	<div><div></div></div>	* 1	0.6158	
16	2	2.54329	0.7400	0.301	<div><div></div></div>	2	0.7400	1 0.25
17	2	3.46957	0.8624	0.148	<div><div></div></div>	2	0.8624	1 0.13

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
18	1	3.57793	0.8596	0.151		1	0.8596	2 0.14
19	1	1.26280	0.6710	0.399		1	0.6710	2 0.33
20	1	0.72964	0.8851	0.122		1	0.8851	2 0.11
21	1	0.72764	0.7409	0.300		1	0.7409	2 0.26
22	1	4.46245	0.7399	0.301		1	0.7399	2 0.26
23	1	1.82571	0.8840	0.123		1	0.8840	2 0.12
24	3	12.09531	0.9935	0.006		3	0.9935	
25	3	11.74292	0.9999	0.000		3	0.9999	
26	1	7.73973	0.9736	0.027		1	0.9736	
27	1	7.15530	0.8480	0.165		1	0.8480	2 0.15
28	1	4.19342	0.9663	0.034		1	0.9663	
29	1	3.15124	0.8821	0.125		1	0.8821	2 0.12
30	1	3.75058	0.9783	0.022		1	0.9783	
31	3	6.45835	0.9649	0.036		3	0.9649	
32	1	1.28966	0.9031	0.102		1	0.9031	
33	3	14.11949	1.0000	0.000		3	1.0000	
34	3	8.88312	0.3616	1.017		* 2	0.6282	
35	3	17.33931	0.9998	0.000		3	0.9998	
36	1	2.39739	0.8363	0.179		1	0.8363	2 0.16
37	2	2.83414	0.8130	0.207		2	0.8130	1 0.15
38	1	3.29080	0.9353	0.067		1	0.9353	
39	1	2.40986	0.7617	0.272		1	0.7617	2 0.24
40	1	6.42383	0.2945	1.223		* 2	0.7022	
41	1	10.26556	0.0885	2.425		* 2	0.9032	
42	2	5.96807	0.8582	0.153		2	0.8582	1 0.13
43	3	3.37171	0.9855	0.015		3	0.9855	
44	?	<i>Puijila darwini</i> (mustelid)				~ - 2	0.9539	
45	?	<i>Puijila darwini</i> (ursid)				~ - 2	0.8878	3 0.11
46	?	<i>Puijila darwini</i> (avg.)				~ - 2	0.9541	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #6:**# of Taxa:** 43**Y, covariates:** $\log(m_b)$, $\log(P_h)$, $\log(P_r)$, $\log(P_u)$, $\log(P_{fe})$, $\log(P_t)$, $\log(P_{fi})$ **X, categories:** SC (1-3)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	4	0
Percent Misclassified	9.302	0
-2LogLikelihood	29.66	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	4.60577	0.2325	1.459	<div><div></div></div>	* 2	0.7381	
2	1	1.72144	0.8541	0.158	<div><div></div></div>	1	0.8541	2 0.15
3	2	5.00030	0.7773	0.252	<div><div></div></div>	2	0.7773	1 0.22
4	3	6.71510	0.9993	0.001	<div><div></div></div>	3	0.9993	
5	3	14.87403	0.9100	0.094	<div><div></div></div>	3	0.9100	
6	3	14.30682	0.5612	0.578	<div><div></div></div>	3	0.5612	2 0.39
7	3	9.05830	0.6383	0.449	<div><div></div></div>	3	0.6383	2 0.34
8	3	25.06525	0.9254	0.078	<div><div></div></div>	3	0.9254	
9	3	1.40191	0.8452	0.168	<div><div></div></div>	3	0.8452	2 0.15
10	3	5.65636	0.9957	0.004	<div><div></div></div>	3	0.9957	
11	1	1.63569	0.5687	0.564	<div><div></div></div>	1	0.5687	2 0.43
12	3	1.65268	0.8932	0.113	<div><div></div></div>	3	0.8932	2 0.10
13	3	4.43748	0.9977	0.002	<div><div></div></div>	3	0.9977	
14	3	33.97009	0.9095	0.095	<div><div></div></div>	3	0.9095	
15	2	0.35642	0.6227	0.474	<div><div></div></div>	2	0.6227	1 0.37
16	2	2.27117	0.6082	0.497	<div><div></div></div>	2	0.6082	1 0.38
17	2	2.80152	0.8773	0.131	<div><div></div></div>	2	0.8773	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
18	1	1.76443	0.7044	0.350		1	0.7044	2 0.30
19	1	0.68453	0.7123	0.339		1	0.7123	2 0.29
20	1	0.95273	0.8769	0.131		1	0.8769	2 0.12
21	1	0.65874	0.7596	0.275		1	0.7596	2 0.24
22	1	3.61039	0.6266	0.467		1	0.6266	2 0.37
23	1	2.21450	0.8101	0.211		1	0.8101	2 0.19
24	3	8.89198	0.9866	0.014		3	0.9866	
25	3	5.83682	0.9991	0.001		3	0.9991	
26	1	6.97112	0.9800	0.020		1	0.9800	
27	1	6.32452	0.9372	0.065		1	0.9372	
28	1	23.47405	0.9465	0.055		1	0.9465	
29	1	2.66619	0.8944	0.112		1	0.8944	2 0.11
30	1	0.85126	0.9043	0.101		1	0.9043	
31	3	8.33810	0.9790	0.021		3	0.9790	
32	1	0.63845	0.8283	0.188		1	0.8283	2 0.17
33	3	14.87324	1.0000	0.000		3	1.0000	
34	3	8.71183	0.2297	1.471		* 2	0.7358	
35	3	11.51364	0.9706	0.030		3	0.9706	
36	1	2.41860	0.7138	0.337		1	0.7138	2 0.29
37	2	2.89147	0.6398	0.447		2	0.6398	1 0.32
38	1	3.49066	0.9252	0.078		1	0.9252	
39	1	1.53169	0.6425	0.442		1	0.6425	2 0.36
40	1	6.65208	0.1955	1.632		* 2	0.7438	
41	1	10.93685	0.0718	2.634		* 2	0.8844	
42	2	6.04572	0.7610	0.273		2	0.7610	1 0.17
43	3	1.52607	0.9804	0.020		3	0.9804	
44	?	<i>Puijila darwini</i> (mustelid)				~ - 3	0.6508	2 0.35
45	?	<i>Puijila darwini</i> (ursid)				~ - 3	0.9690	
46	?	<i>Puijila darwini</i> (avg.)				~ - 3	0.8843	2 0.12

"~" indicates excluded row; "*" indicates misclassified

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
14	2	4.11265	0.5727	0.557		2	0.5727	1 0.43
15	2	2.21803	0.9253	0.078		2	0.9253	
16	2	3.32260	0.9943	0.006		2	0.9943	
17	1	3.18219	0.9714	0.029		1	0.9714	
18	1	1.55403	0.7924	0.233		1	0.7924	2 0.21
19	1	0.64625	0.9588	0.042		1	0.9588	
20	1	1.37521	0.8445	0.169		1	0.8445	2 0.16
21	1	5.86624	0.5612	0.578		1	0.5612	2 0.44
22	1	1.58751	0.9584	0.043		1	0.9584	
23	4	1.60026	1.0000	0.000		4	1.0000	
24	3	11.73637	1.0000	0.000		3	1.0000	
25	1	10.05195	0.9999	0.000		1	0.9999	
26	1	7.08926	0.9823	0.018		1	0.9823	
27	1	6.00700	0.9973	0.003		1	0.9973	
28	1	2.87848	0.9734	0.027		1	0.9734	
29	1	3.39158	0.9985	0.002		1	0.9985	
30	3	7.47482	1.0000	0.000		3	1.0000	
31	1	0.96038	0.9795	0.021		1	0.9795	
32	3	13.04336	1.0000	0.000		3	1.0000	
33	3	8.25494	0.9923	0.008		3	0.9923	
34	3	15.49944	1.0000	0.000		3	1.0000	
35	1	4.03677	0.8696	0.140		1	0.8696	2 0.13
36	2	5.80644	0.9179	0.086		2	0.9179	
37	1	2.78586	0.9880	0.012		1	0.9880	
38	1	4.50049	0.8047	0.217		1	0.8047	2 0.20
39	3	4.21634	0.9965	0.004		3	0.9965	
40	?	<i>Puijila darwini</i> (mustelid)				~ - 2	0.9663	
41	?	<i>Puijila darwini</i> (ursid)				~ - 3	0.9314	
42	?	<i>Puijila darwini</i> (avg.)				~ - 2	0.5926	3 0.41

"~" indicates excluded row; '*' indicates misclassified

ANALYSIS #8:

of Taxa: 39 (no bears)

Y, covariates: P_h, P_r, P_u, P_{fe}, P_t, P_{fi}

X, categories: SC (1-4)

Canonical Plot

Discriminant Scores

		Training		Excluded			
Number Misclassified		5		0			
Percent Misclassified		12.82		0			
-2LogLikelihood		37.37					
Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred) Others
1	1	2.18639	0.7609	0.273	<div><div></div></div>	1	0.7609 2 0.24
2	2	6.46777	0.5434	0.610	<div><div></div></div>	2	0.5434 3 0.44
3	3	5.07871	0.9761	0.024	<div><div></div></div>	3	0.9761
4	3	12.86131	0.9890	0.011	<div><div></div></div>	3	0.9890
5	3	8.09767	0.9750	0.025	<div><div></div></div>	3	0.9750
6	4	0.41112	1.0000	0.000	<div><div></div></div>	4	1.0000

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
7	3	18.26902	0.0023	6.081		* 2	0.6977	1 0.30
8	3	3.61833	0.9138	0.090		3	0.9138	
9	3	7.28227	0.9868	0.013		3	0.9868	
10	1	2.68931	0.8465	0.167		1	0.8465	2 0.15
11	3	4.57647	0.6678	0.404		3	0.6678	2 0.28
12	3	7.04872	0.9900	0.010		3	0.9900	
13	3	23.29522	0.9091	0.095		3	0.9091	
14	2	4.08655	0.1539	1.872		* 1	0.8460	
15	2	1.50277	0.6880	0.374		2	0.6880	3 0.22
16	2	2.08306	0.6714	0.398		2	0.6714	1 0.32
17	1	3.17723	0.7907	0.235		1	0.7907	2 0.21
18	1	1.20401	0.5636	0.573		1	0.5636	2 0.43
19	1	0.64077	0.7224	0.325		1	0.7224	2 0.28
20	1	0.97640	0.6702	0.400		1	0.6702	2 0.33
21	1	3.86602	0.7230	0.324		1	0.7230	2 0.28
22	1	1.58625	0.7029	0.353		1	0.7029	2 0.30
23	4	0.41112	1.0000	0.000		4	1.0000	
24	3	11.04724	0.8749	0.134		3	0.8749	2 0.12
25	1	3.67530	0.7615	0.272		1	0.7615	2 0.23
26	1	5.39743	0.2325	1.459		* 2	0.7343	
27	1	3.60572	0.5468	0.604		1	0.5468	2 0.45
28	1	2.26030	0.3753	0.980		* 2	0.5901	
29	1	2.97230	0.9385	0.063		1	0.9385	
30	3	7.30728	0.9739	0.026		3	0.9739	
31	1	0.95670	0.8000	0.223		1	0.8000	2 0.20
32	3	11.15172	0.9992	0.001		3	0.9992	
33	3	8.19461	0.4442	0.812		* 2	0.4723	
34	3	15.40235	0.9969	0.003		3	0.9969	
35	1	2.32392	0.9157	0.088		1	0.9157	
36	2	5.76563	0.5304	0.634		2	0.5304	1 0.30 3 0.14
37	1	2.20882	0.6008	0.509		1	0.6008	2 0.40
38	1	2.65178	0.8822	0.125		1	0.8822	2 0.12
39	3	3.66241	0.9115	0.093		3	0.9115	
40	?		<i>Puijila darwini</i>			~ - 2	0.9159	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #9:**# of Taxa:** 27**Y, covariates:** Log (m_b), S_h , S_r , S_u , S_{fe} , S_t , S_{fi} , C_h , C_r , C_u , C_{fe} , C_t , C_{fi} , Min_h , Min_r , Min_u , Min_{fe} , Min_t , Min_{fi} **X, categories:** SC (1-4)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	1	0
Percent Misclassified	3.704	0
-2LogLikelihood	1.802	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	10.41746	0.9986	0.001	<input type="text"/>	1	0.9986	
2	3	18.60200	1.0000	0.000	<input type="text"/>	3	1.0000	
3	3	19.94524	1.0000	0.000	<input type="text"/>	3	1.0000	
4	3	18.74777	1.0000	0.000	<input type="text"/>	3	1.0000	
5	4	9.11832	1.0000	0.000	<input type="text"/>	4	1.0000	
6	3	21.17332	1.0000	0.000	<input type="text"/>	3	1.0000	
7	3	20.92414	1.0000	0.000	<input type="text"/>	3	1.0000	
8	3	18.92942	1.0000	0.000	<input type="text"/>	3	1.0000	
9	1	10.21564	0.9992	0.001	<input type="text"/>	1	0.9992	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
10	3	15.31169	1.0000	0.000		3	1.0000	
11	3	18.63000	1.0000	0.000		3	1.0000	
12	3	15.85525	1.0000	0.000		3	1.0000	
13	2	15.92627	0.9984	0.002		2	0.9984	
14	2	15.69304	1.0000	0.000		2	1.0000	
15	1	10.00526	0.9983	0.002		1	0.9983	
16	4	9.11832	1.0000	0.000		4	1.0000	
17	3	19.11103	1.0000	0.000		3	1.0000	
18	3	17.03041	1.0000	0.000		3	1.0000	
19	3	21.33697	1.0000	0.000		3	1.0000	
20	3	17.35498	1.0000	0.000		3	1.0000	
21	3	19.65953	1.0000	0.000		3	1.0000	
22	2	15.54646	1.0000	0.000		2	1.0000	
23	1	18.08188	0.9989	0.001		1	0.9989	
24	1	15.93592	0.9991	0.001		1	0.9991	
25	1	12.68523	0.9999	0.000		1	0.9999	
26	2	15.04092	0.4092	0.894		* 1	0.5908	
27	3	16.60354	1.0000	0.000		3	1.0000	
28	?	<i>Puijila darwini</i> (mustelid)				~ - 3	1.0000	
29	?	<i>Puijila darwini</i> (ursid)				~ - 3	1.0000	
30	?	<i>Puijila darwini</i> (avg.)				~ - 3	1.0000	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #10:**# of Taxa:** 27

Y, covariates: $\log(m_b)$, $\log(S_h)$, $\log(S_r)$, $\log(S_u)$, $\log(S_{fe})$, $\log(S_t)$, $\log(S_{fi})$, $\log(C_h)$, $\log(C_r)$, $\log(C_u)$, $\log(C_{fe})$, $\log(C_t)$, $\log(C_{fi})$, $\log(\text{Min}_h)$, $\log(\text{Min}_r)$, $\log(\text{Min}_u)$, $\log(\text{Min}_{fe})$, $\log(\text{Min}_t)$, $\log(\text{Min}_{fi})$

X, categories: SC (1-4)

Canonical Plot **Discriminant Scores**

	Training	Excluded
Number Misclassified	0	0
Percent Misclassified	0	0
-2LogLikelihood	3e-8	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot	-Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	14.58813	1.0000	0.000	<input type="text"/>		1	1.0000	
2	3	16.20720	1.0000	0.000	<input type="text"/>		3	1.0000	
3	3	20.37092	1.0000	0.000	<input type="text"/>		3	1.0000	
4	3	21.05425	1.0000	0.000	<input type="text"/>		3	1.0000	
5	4	10.21319	1.0000	0.000	<input type="text"/>		4	1.0000	
6	3	20.07836	1.0000	0.000	<input type="text"/>		3	1.0000	
7	3	13.93836	1.0000	0.000	<input type="text"/>		3	1.0000	
8	3	18.05779	1.0000	0.000	<input type="text"/>		3	1.0000	
9	1	10.63920	1.0000	0.000	<input type="text"/>		1	1.0000	
10	3	18.29525	1.0000	0.000	<input type="text"/>		3	1.0000	
11	3	20.66119	1.0000	0.000	<input type="text"/>		3	1.0000	
12	3	19.80932	1.0000	0.000	<input type="text"/>		3	1.0000	
13	2	10.90047	1.0000	0.000	<input type="text"/>		2	1.0000	
14	2	14.72119	1.0000	0.000	<input type="text"/>		2	1.0000	
15	1	12.64222	1.0000	0.000	<input type="text"/>		1	1.0000	
16	4	10.21319	1.0000	0.000	<input type="text"/>		4	1.0000	
17	3	20.37186	1.0000	0.000	<input type="text"/>		3	1.0000	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
18	3	20.05189	1.0000	0.000		3	1.0000	
19	3	17.20238	1.0000	0.000		3	1.0000	
20	3	15.14713	1.0000	0.000		3	1.0000	
21	3	21.20626	1.0000	0.000		3	1.0000	
22	2	10.24512	1.0000	0.000		2	1.0000	
23	1	16.54950	1.0000	0.000		1	1.0000	
24	1	15.61802	1.0000	0.000		1	1.0000	
25	1	15.19755	1.0000	0.000		1	1.0000	
26	2	14.03791	1.0000	0.000		2	1.0000	
27	3	18.98216	1.0000	0.000		3	1.0000	
28	?	<i>Puijila darwini</i> (mustelid)				~ - 2	1.0000	
29	?	<i>Puijila darwini</i> (ursid)				~ - 2	1.0000	
30	?	<i>Puijila darwini</i> (avg.)				~ - 2	1.0000	

"~" indicates excluded row; "*" indicates misclassified

ANALYSIS #11:

of Taxa: 27

Y, covariates: $S_h, S_r, S_u, S_{fe}, S_t, S_{fi}, C_h, C_r, C_u, C_{fe}, C_t, C_{fi}, Min_h, Min_r, Min_u, Min_{fe}, Min_t, Min_{fi}$ **X, categories:** SC (1-4)**Canonical Plot** **Discriminant Scores**

	Training	Excluded
Number Misclassified	1	0
Percent Misclassified	3.704	0
-2LogLikelihood	1.469	

Row	SC	SqDist(Actual)	Prob(Actual)	-Log(Prob)	Plot -Log(Prob)	Predicted SC	Prob(Pred)	Others
1	1	8.79288	0.9991	0.001	<input type="text"/>	1	0.9991	
2	3	18.56893	1.0000	0.000	<input type="text"/>	3	1.0000	
3	3	19.86298	1.0000	0.000	<input type="text"/>	3	1.0000	
4	3	18.43512	1.0000	0.000	<input type="text"/>	3	1.0000	
5	4	8.24702	1.0000	0.000	<input type="text"/>	4	1.0000	
6	3	21.16022	1.0000	0.000	<input type="text"/>	3	1.0000	
7	3	20.14669	1.0000	0.000	<input type="text"/>	3	1.0000	
8	3	18.92212	1.0000	0.000	<input type="text"/>	3	1.0000	
9	1	9.69021	0.9988	0.001	<input type="text"/>	1	0.9988	
10	3	14.45452	1.0000	0.000	<input type="text"/>	3	1.0000	
11	3	18.55849	1.0000	0.000	<input type="text"/>	3	1.0000	
12	3	15.68870	1.0000	0.000	<input type="text"/>	3	1.0000	
13	2	15.82250	0.9980	0.002	<input type="text"/>	2	0.9980	
14	2	14.37008	1.0000	0.000	<input type="text"/>	2	1.0000	
15	1	6.83623	0.9957	0.004	<input type="text"/>	1	0.9957	
16	4	8.24702	1.0000	0.000	<input type="text"/>	4	1.0000	
17	3	18.82078	1.0000	0.000	<input type="text"/>	3	1.0000	