

Evidence for independent acquisition of aquatic specializations in pinnipeds (seals, sea lions, and walruses): insights from study of the phylogenetic position, locomotor behaviour and description of the stem pinniped, *Puijila darwini*

by

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Abstract

Monophyly of pinnipeds (seals, sea lions, and walruses) is well-established. However, it is difficult to reconcile a monophyletic origin of pinnipeds with the disparate locomotory modes and associated skeletal morphologies observed between the extant families. In this study, the skeletal anatomy of *Puijila darwini*, a key putative stem pinniped from Canada's High Arctic, is fully described. A biomechanical analysis, using functional limb indices of extant carnivorans to predict locomotory modes in extinct taxa, confirms the aquatic adaptations of *Puijila*, and identifies it as a forelimb-dominated swimmer. Phylogenetic analyses of molecular and morphological data in isolation recover *Puijila* as a stem pinniped, and provide strong support for pinniped monophyly. However, a phylogenetic analysis combining molecular and morphological data together recovers an unconventional topology, suggesting the molecular and morphological data are incongruent. Closer scrutiny of previously-proposed pinniped synapomorphies suggests many features shared between seals, sea lions, and walruses arose in parallel.

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Chapter 1: Introduction

Phocids (seals), otariids (sea lions), and odobenids (walruses) are the highly aquatically adapted extant lineages included within the Pinnipedia. Monophyly of pinnipeds has long been contentious, owing to the morphological and biomechanical differences observed between the three extant lineages. Analyses of molecular data have provided clarity on the relationships between modern taxa, providing support for a monophyletic Pinnipedia. In recent years, the fossil record has also co-operated, through the discovery of well-preserved cranial and postcranial material of fossil members of the extant lineages (Kohn, 1994; Deméré and Berta, 2001, 2002, 2005; Koretsky and Holec, 2002; Koretsky et al., 2016; Boessenecker and Churchill 2013; Dewaele et al., 2017; Velez-Juarbe, 2017). However, the problems associated with our continued lack of a robust understanding of pinniped phylogeny and evolution have been exacerbated by the unexpectedly unspecialized morphologies displayed by some of these recently described fossil phocids, otariids, and odobenids. These fossil taxa can comfortably be placed in each of the modern families, yet they lack many purported pinniped synapomorphies, and do not depart significantly from the morphology displayed by early-diverging stem taxa, like *Enaliarctos*.

Enaliarctos, likely a fully-flipped form, was previously envisioned as a link between otariids and ursids (Mitchell and Tedford, 1973; Tedford, 1976). More recently, *Enaliarctos* has been allocated to the stem of a monophyletic Pinnipedia (Berta et al., 1990, Berta, 1991; Berta and Wyss, 1994). The gap between *Enaliarctos* and terrestrial carnivorans has been difficult to fill with fossil taxa, obscuring the relationships between pinnipeds and other members of the arctoid clade (e.g., bears, weasels, pinnipeds, and

their kin). However, in 2009, Rybczynski et al. (2009) reported the discovery of a new semi-aquatic Carnivoran – *Puijila darwini* – from lacustrine deposits in Canada’s High Arctic. A preliminary phylogenetic analysis identified *Puijila* as a stem pinniped, alongside *Enaliarctos* and *Potamotherium*, an enigmatic freshwater form from the Oligocene and Miocene of Europe. However, the precise phylogenetic relationships of *Puijila darwini*, within the greater arctoid clade, was not formally tested, so its precise relationship to pinnipeds, in a broader phylogenetic context, remains incompletely understood.

The present study builds on the original study of *Puijila darwini* by completing a detailed description and subjecting it to comprehensive phylogenetic analyses sampling both extant and fossil arctoids from all known families.

In chapter two, NUFV-405, the holotype skeleton of *Puijila darwini*, is described. High resolution micro-computed tomography scans allow for a detailed description of the interior features of the skull. Comparisons are made between NUFV-405 and the skeletons of other arctoids, including *Potamotherium* and *Enaliarctos*, a pair of fossil arctoids also implicated in the origin and divergence of pinnipeds. Accompanying the description is a brief biomechanical analysis, building on the work of Samuels et al., (2013). The biomechanical analysis employs functionally-informative measurements of the postcranial skeleton to discriminate between taxa displaying hindlimb-dominated and forelimb-dominated aquatic locomotion. The predictive power of the discriminant function analysis is used to predict the likely locomotory mode of NUFV-405, and to make inferences on the plesiomorphic swimming condition in pinnipeds.

In chapter three, a phylogenetic analysis is performed to determine the relationships of *Puijila* to other arctoids, and test hypotheses concerning pinniped evolution. Several different datasets, including morphology- and molecular-based datasets, are used to test the evolutionary relationships of pinnipeds. These analyses use Bayesian inference and Maximum Parsimony to reconstruct possible topologies. The resulting topologies yielded from different analyses are then compared, to further describe the discrepancy between morphological and molecular results. Finally, the datasets are combined in a Total Evidence Analysis. Divergence time estimation is performed to provide additional insights into the timing of the aquatic transition of pinnipeds.

Chapter 2: A complete description of the transitional pinniped, *Puijila darwini*, and inferences on the evolution of aquatic locomotion in pinnipeds

Abstract

In 2009, Rybczynski and colleagues reported the discovery of *Puijila darwini*, a putative stem pinniped from the Miocene of Canada's High Arctic. A brief description of the otter-like *Puijila* was complemented with a preliminary phylogenetic analysis that united *Puijila* in a clade with *Enaliarctos* (the earliest flippered pinniped), *Potamotherium* (an arctoid of unresolved phylogenetic position) and *Amphicticeps* (a terrestrial Carnivoran from the Oligocene of Eurasia previously allied with ursids (bears)). The present study offers a complete description of *Puijila* and further identifications of new potentially taxonomically informative traits shared by *Puijila* and other proposed stem pinnipeds. The skeletal and dental anatomy of *Puijila* are compared to those of pinnipeds, other semi-aquatic carnivorans and other taxa implicated in the divergence of pinnipeds. High-resolution micro-computed tomography allowed for observation of the internal anatomy of the skull of *Puijila*, which is otherwise obscured by matrix. To reconstruct aspects of *Puijila*'s locomotory behaviour, a pair of biomechanical analyses are performed. Both analyses involve using linear measurements of the post-cranial skeleton in extant taxa to predict the locomotory mode of extinct taxa. The results of the two analyses agree that *Puijila* was well-adapted to an aquatic existence, more so than any living lutrine. However, the results of the analyses disagree on the aquatic specializations of *Puijila* (e.g., forelimb- vs hindlimb-dominated swimming), making it difficult to make inferences on the plesiomorphic swimming

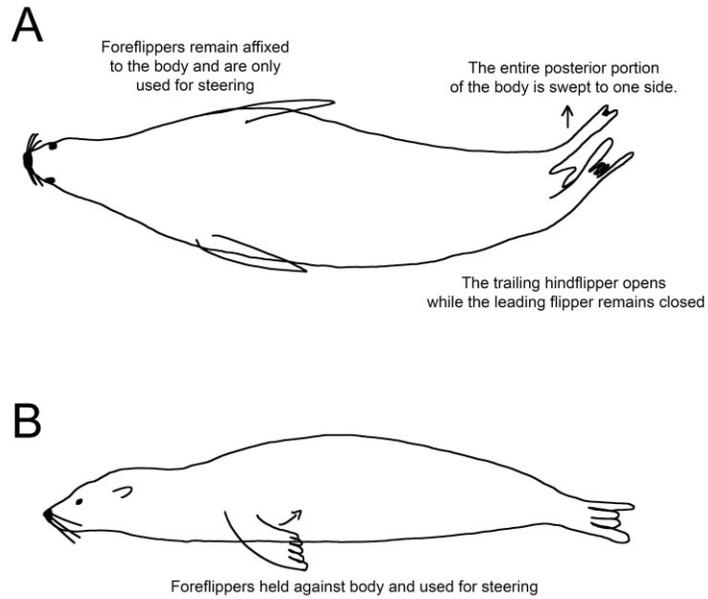
condition in pinnipeds.

Introduction

Pinnipedia is a monophyletic clade of flippered marine mammals represented by three extant families – Phocidae (earless seals), Otariidae (sea lions and fur seals), and Odobenidae (walrus) (Berta and Sumich, 2005). These groups are highly adapted for swimming, but exhibit disparate swimming modes and divergent postcranial morphologies. Phocids laterally undulate the posterior portion of their spinal columns, generating thrust through the resultant lateral sweeps of their hind-flippers (Fish, 1988). Contrasting the phocid style of pelvic oscillations (Figure 1.1), otariids engage in pectoral oscillations (Figure 1.2), relying on their large paddle-like foreflippers to provide thrust so they may figuratively fly through their aquatic medium like a bird in flight (Fish, 1988). The hindflippers of otariids are relegated to the task of steering. The single extant odobenid species (*Odobenus rosmarus*) displays both locomotory styles, engaging in phocid-like pelvic oscillations at high velocities and otariid-like pectoral swimming at slow speeds (Pierce, 2011).

Whereas the fossil record of the land-to-sea transition is well-documented in many secondarily aquatic mammals, that of early-diverging pinnipeds is relatively sparse, offering few well-preserved transitional fossils (Mitchell and Tedford, 1973; Berta, 1991; 1994a; Rybczynski et al., 2009). Due to this paucity of transitional pinniped forms, it remains difficult to reconcile how such divergent locomotory modes and associated morphologies arose between such closely related lineages.

The fossil carnivore *Puijila darwini* is known from the Early Miocene of Canada's High Arctic. *Puijila darwini* is represented by a single individual – an adult male – which was briefly described by Rybczynski et al. (2009). An



Redrawn from Fish (1993)

Figure 1.1. Illustration of swimming style employed by phocids. A=dorsal view, B=lateral view.

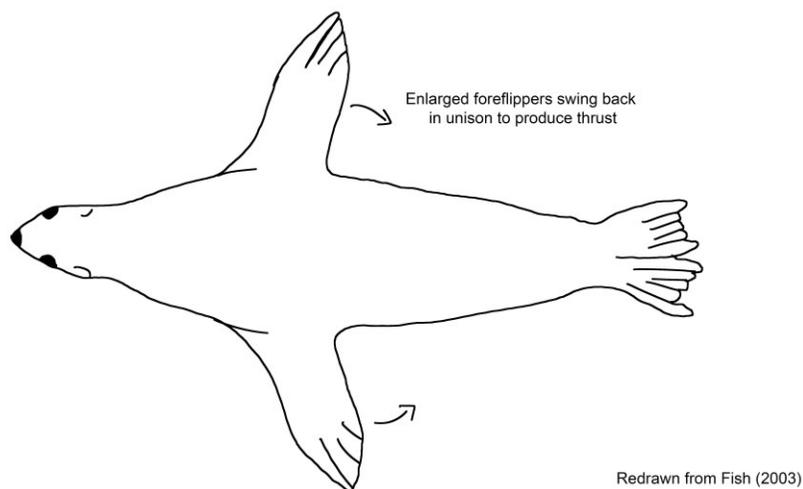


Figure 1.2. Illustration of swimming style employed by otariids in dorsal view.

interactive website devoted to *Puijila* accompanied this publication. Since this publication, additional postcranial material of *Puijila darwini* has been uncovered from the same locality – the Houghton Crater of Devon Island, located in the Canadian territory of Nunavut. This postcranial material is attributable to the same individual – NUFV 405.

Puijila darwini displays an osteological morphology suggestive of a semi-aquatic existence. In a parsimony analysis, applied to a matrix of 26 taxa and 42 characters, modified from Wang (2005), *Puijila* was recovered alongside *Potamotherium* as a pinnipedimorph, bridging the gap between the terrestrial *Amphicticeps* and the fully-flipperered stem pinniped *Enaliarctos* (Rybczynski et al., 2009). *Potamotherium* and *Enaliarctos* are well-represented in the fossil record, replete with published descriptions of their entire skeletons (Savage, 1957; Berta et al., 1989).

Enaliarctos, known from five species distributed throughout the north pacific, has been well-studied from a number of perspectives. The internal anatomy of *Enaliarctos*

was briefly described through high resolution micro-computed tomography (HR μ CT) (Cullen et al., 2014), and endocranial casts have received elaborate descriptions (Mitchell and Tedford, 1973, Hunt and Barnes, 1994). Though there is disagreement over its phylogenetic position (Mitchell and Tedford, 1973) *Enaliarctos* is typically recovered as a stem pinniped, ancestral to both otarioids (otariids + odobenids) and phocids (Berta et al., 1989; Berta and Wyss, 1994). Berta et al. (1989) presented a description of a nearly complete postcranial skeleton of *Enaliarctos*, offering remarks on its musculature and suggesting it swam in a less specialized way than living pinnipeds. Berta and Adam (2001) used extant phylogenetic bracketing to reconstruct *Enaliarctos* as a forelimb-dominated swimmer. Bebej (2009) performed a Principal Components Analysis (PCA) on linear measurements of trunk and limb elements in extant semi-aquatic mammals to infer its swimming behaviour, producing an alternative reconstruction of *Enaliarctos* as a hindlimb-dominated swimmer. Furbish (2015) agreed that *Enaliarctos* favoured its hindlimbs, but identified *Enaliarctos* as a combination swimmer.

On the other hand, study of *Potamotherium* has dwindled since the 1980's, when Wyss (1987, 1988, 1991) decoupled the proposed evolutionary relationship between *Potamotherium* and Phocidae, relegating the enigmatic *Potamotherium* to Arctoidea *incertae sedis* (Flynn, 1988). *Potamotherium* is known from thousands of isolated specimens from a small number of late Oligocene and early Miocene sites in Europe (Savage, 1957), and a few scattered mandibles and postcranial elements in North America (Ginsburg, 1999; Qui, 2003), though no complete skeleton of a single individual has been described. *Potamotherium* awaits a description of its internal anatomy via HR μ CT, though its auditory and basicranial regions have been well-studied (Savage,

1957; Tedford, 1976; Wyss, 1987, 1988, 1991; Schmidt-Kittler, 1981; de Muizon, 1981a). *Potamotherium* has also been variously allocated to Oligobuninae (Baskin, 1998), a possibly paraphyletic family of late Oligocene - early Miocene paleomustelids from North America, as well as the Semantoridae (Sato et al., 2010).

Membership within Semantoridae and the phylogenetic placement of the group within arctoids are controversial, but largely centred around the enigmatic *Semantor macrurus*, and its role in pinniped systematics. *Semantor macrurus* (Orlov, 1933) like *Puijila*, is a fresh-water taxon represented by just a single individual – the posterior half of the skeleton, and a single humerus (found in a later excavation, but attributed to the same individual) (Kirpichnikov, 1955). *Semantor* was uncovered from Early Pliocene deposits in Kazakhstan, an area which would have been submerged by the Paratethys sea. *Semantor* has been referred to as “phocid-like” (Flynn, 1988) in general proportions, and was thought to have some relevance to phocid origins (Orlov, 1933; Kirpichnikov, 1955; de Muizon, 1982; Barnes, 1985), but does not possess any of the known phocid synapomorphies (Orlov, 1933; Thenius, 1949). Regardless of its phylogenetic affinities, the postcranial morphology of *Semantor* bespeaks a level of aquatic adaptation more advanced than that of *Potamotherium*, and possibly even *Enaliarctos*. Whereas the hindlimb elements of *Semantor* have not received a thorough descriptive treatment, casts available in the American Museum of Natural History permit a comparison between *Semantor* and *Puijila*.

Later-diverging fossil pinnipedimorphs, including those within the crown group, are often represented only by skulls, dentition, and fragmentary or isolated postcranial elements. However, detailed descriptions of specimens possessing nearly complete

postcranial skeletons have been produced for a variety of genera within the four pinniped families: Phocidae (*Devinophoca* – Rahmat and Koretsky, 2016; *Acrophoca* – de Muizon, 1981; *Leptophoca* – Koretsky et al., 2002; Dewaele et al., 2017), Otariidae (*Thalassoleon* – Deméré and Berta, 2005), Odobenidae (*Imagotaria* – Repenning and Tedford, 1977) and the extinct Desmatophocidae (*Allodesmus* – Mitchell, 1966; Barnes, 2008).

Speculative accounts of locomotory behaviour have often accompanied these skeletal descriptions (de Muizon, 1981; Deméré and Berta, 2005; Dewaele et al., 2017), but few studies (Bebej, 2009) have quantitatively explored the evolution of swimming behaviour in pinnipeds, and those that have done so have largely restricted their analyses to crown pinnipeds (Pierce et al., 2011). Nevertheless, such studies have produced valuable insights into the evolution of forelimb- and hindlimb-dominated swimming in pinnipeds. The current study attempts to provide further resolution to this question by attempting to infer the type of swimming behaviour employed by *Puijila* and *Potamotherium*. These taxa bridge the gap between fully terrestrial carnivorans and the fully-flipped, obligately-aquatic *Enaliarctos*, allowing for inferences on the plesiomorphic swimming condition in pinnipeds.

Ecomorphological analyses of terrestrial carnivorans have previously been used to predict the locomotory modes of extinct taxa (Van Valkenburgh, 1987; Anyonge, 1996; Heinrich and Rose, 1997; Samuels et al., 2013). Samuels et al. (2013) developed a set of functional indices, based on linear measurements of limb elements and their associated muscle attachments, to identify osteological correlates of various locomotory modes. This dataset, when subject to a discriminant function analysis, was able to accurately predict

locomotory group membership, and was particularly successful at identifying semi-aquatic carnivorans. The present study supplements this dataset by collecting additional data of extant pinnipeds, and observing if it can effectively discriminate between hindlimb-dominated and forelimb-dominated swimmers. The dataset and methodology of Bebej (2009) are also employed to witness how *Puijila* compares to other semi-aquatic and aquatic taxa across the breadth of Mammalia.

Materials and Methods

Specimens Examined

The following taxa were examined in this study for the comparative description: *Potamotherium valletoni*, *Potamotherium miocenicum*, *Enaliarctos mealsi*, *Enaliarctos mitchelli*, *Enaliarctos emlongi*, *Enaliarctos tedfordi*, *Enaliarctos barnesi*, *Semantor macrurus*, *Pteronarctos godertae*, *Desmatophoca oregonensis*, *Eumetopias jubatus*, *Halichoerus grypus*, *Proneotherium repenningi*, *Odobenus rosmarus*, *Megalictis ferox*, *Amphicticeps shackelfordi*, *Allocyon loganensis*, *Kolponomos newportensis*. See Table 1 for complete list of specimens and specimen numbers of the material examined here.

The dataset of Samuels et al. (2013) included terrestrial and semi-aquatic carnivorans (equivalent to the paraphyletic “fissipedia”; an informal grouping of non-pinniped-carnivorans) displaying a wide range of sizes, geographical distributions, and locomotory modes. To supplement this data set, novel data was collected on a selection of pinniped taxa, sampling all three extant families. Only measurements from adult specimens (with fully-fused proximal and distal epiphyses) were taken. The dearth of available adult specimens did not allow us to selectively examine wild-caught

individuals. Table 18 and Table 20 (Appendix C) include all pinniped specimens examined for the biomechanical analysis.

Institutional Abbreviations

CMN = Canadian Museum of Nature

LACM = Natural History Museum of Los Angeles County

NUFV = Nunavut Fossil Vertebrate Collection

ROM = Royal Ontario Museum

USNM = Smithsonian Institution National Museum of Natural History

Imaging

The skeletal remains of NUFV-405 were surface scanned using an Arius 3D (Vancouver, Canada) surface laser scanner. The scans were reassembled in Pointstream (v3.2.0.0; Arius, Vancouver, Canada), and converted into triangulated polymesh surfaces with Paraform software (v3.1; Paraform Inc.; Santa Clara, California, USA). The bones are naturally very dark-coloured. To improve image quality, the colour was digitally-removed. Fragments of broken skeletal elements were digitally reassembled using 3D Studio Max (Autodesk; San Rafael, California, USA). The figured skeletal elements were uploaded into Amira v.5 (Visage Imaging; Hillsboro, Oregon, USA), and the ‘boundary ids’ option was selected to colour the bones, with no further modifications to colour.

High Resolution micro-Computed Tomography (HR μ CT) allowed us to acquire digital volumetric data of the cranium of NUFV-405. The anterior portion of the cranium was scanned with a Skyscan 1173 (Bruker; Montréal, Quebec, Canada) at Carleton

University, in the tomography lab of Dr. Gaidies. The posterior portion of the cranium was scanned at the Center for Qualitative Imaging at Pennsylvania State University, Pennsylvania, USA. The OMNI-X HD600 industrial system and the X-TEK microfocus X-Ray tube were used. Energy settings were 180kV and 0.3 mA. The field of view (FOV) was 61mm. 1440 projections were collected with five samples averaged per projection. An independent scan of the inner ear was also performed at a higher resolution, utilizing the same energy settings, but a FOV of 30.72mm.

To prepare them for analysis, the original HR μ CT TIFF images were downsampled and reduced to 8-bit images in ImageJ (Schneider et al., 2012). Scans were imported into Amira v.5 (Visage Imaging, Hillsboro, Oregon, USA) as a series of stacked images. To isolate and segment the endosseous bony labyrinth, the LabelFields module and the Segmentation Editor were used. Virtual endocasts were visualized by applying SurfaceGen and SurfaceView modules to the segmented data.

Measurements

All measurements in the present study are taken with digital calipers to the nearest 0.01 mm. Various measurements regarding the skull, dentition, and limb lengths are listed in Tables 2-5.

The first proxy follows the approach of Samuels et al. (2013), wherein a set of functional indices, based on linear measurements of limb elements, and their respective muscular attachment sites, was developed to identify osteological correlates of various locomotory modes. These indices are meant to reflect the mechanical properties of these skeletal elements and associated primary locomotor muscles. Definitions of these

functional indices and the associated raw measurements are described in Samuels et al., (2013). Samuels et al. (2013) included terrestrial and semi-aquatic taxa (“fissipeds”), but did not include pinnipeds, who are significantly more modified for an aquatic existence than any “fissipeds”. In the present study, additional data is collected for a selection of pinniped taxa (Appendix B: Table 16). Table 17 (Appendix B) lists the functional indices and their scores for specimens added in the present analysis.

The second proxy follows the methodology of Bebej (2009), itself based on the work of Gingerich (2003). The original analysis utilised 14 linear measurements of trunk and limb elements to capture the overall skeletal proportions of mammals displaying some degree of aquatic adaptation, including 16 pinniped taxa. Bebej (2009) built upon this work by collecting data for an additional eight pinniped species. Distribution throughout this morphospace was then used to predict the locomotory behaviours of *Enaliarctos mealsi* and *Allodesmus kelloggi*. Measurements used in the present study for *Puijila darwini* and *Potamotherium valletoni*, are listed in Table 18 (Appendix B), and follow the guidelines of Bebej (2009).

Data Analysis

To reconstruct the locomotory capabilities of *Puijila darwini* and make inferences on the plesiomorphic swimming condition of pinnipeds, several different proxies were employed, building on the work of Samuels et al. (2013), and exploiting the predictive power of analyses from Bebej (2009).

Expanding the work of Samuels et al. (2013), a discriminant function analysis (DFA) is run to further discriminate between semi-aquatic and aquatic taxa, and to

separate forelimb-dominated swimmers from hind-limb dominated swimmers. Two stepwise DFA's were performed. The first DFA included the expanded dataset, sampling both 'fissipeds' and pinnipeds. The second DFA limited the scope to pinnipeds. The stepwise models included variables with F probability <0.05 and excluded variables with F probability >0.1. Scatter plots of DF1 and DF2 scores were produced to better visualize separation of locomotor groups and the placement of *Puijila* and *Potamotherium*. All data analyses were performed with IBM SPSS Statistics 19 (IBM, Armonk, USA)

Beyond adding additional pinnipeds, Bebej (2009) further expanded the work of Gingerich (2003) by running an additional set of analyses, a principal components analysis (PCA) and a DFA, exclusive of non-pinnipeds, to better define the morphospace occupied by pinnipeds. As part of the present analysis, *Puijila darwini* and *Potamotherium valletoni* were added as supplemental taxa and plotted with the taxa included in Bebej (2009). Their principal component (PC) scores were calculated using the eigenvector coefficients produced by the original PCAs. Likewise, discriminant scores were calculated for *Puijila* and *Potamotherium* by summing the constant and the products of the ln-transformed measurements of the unstandardized discriminant function coefficients for each variable.

Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Order-Group Taxon Mustelida Tedford, 1976

Clade Pinnipedimorpha (Berta et al., 1989)

Puijila darwini (Rybczynski et al., 2009)

Type Specimen

NUFV-405, nearly complete skeleton and includes the following elements. A partial cranium lacks most of the skull roof, the posterior portion of the palate, the paroccipital processes, the right occipital condyle, the right zygomatic bar, and the ventral extensions of the post-glenoid processes. The upper dentition is nearly complete though the right P¹, P³, and M², and the left P² and M² are not in-situ, and the right and left I¹s and I²s are outright missing. The left and right mandibles are nearly complete, lacking the dorsal portion of the ramus and right and left I²s. Only the left and right P⁴ and the right M¹ are in-situ. Measurements associated with the cranium, the upper dentition, and the lower dentition and mandible are listed in Tables 2, 3, and 4, respectively.

All cervical, thoracic, and lumbar vertebrae are at least partially accounted for, though many lack neural spines and incompletely preserve their transverse processes. Fourteen caudal vertebrae are well-preserved, but the distal-most caudal vertebrae are not present. The sacrum is nearly complete, but lacks spinous processes. The sternbrae is nearly complete, though the anterior half of the manubrium is missing. The set of ribs is incomplete, and individual ribs are highly fragmentary. The scapulae are present, but lack the majority of the supraspinous fossa. The innominates are nearly complete, but lack portions of the pubis and ischium. The preserved appendicular skeleton includes the left

and right humerii, radii, ulnae, carpals, metacarpals, fore phalanges, femora, tibiae, fibulae, tarsals, metatarsals, and hind phalanges. Measurements associated with the appendicular skeleton are provided in Table 5.

Type Locality

The holotype was collected from the Houghton Crater, on Devon Island, in the Canadian territory of Nunavut (75°22' N, 89° 40' W).

Formation and Age

The Houghton Crater is an impact structure, spanning 23 km in diameter, and dated at 23.4^{±1} million years ago (Jessberger, 1988). This age is supported by the faunal and floral remains associated with the paleolacustrine sediments, which indicate a late Oligocene to middle Miocene age (Whitlock and Dawson, 1990) (though see Jessberger et al., 2005, for an alternate date). The fossiliferous Houghton Formation is comprised of unconsolidated sediments situated within the crater. These sediments are intermittently exposed over an 8.62 km² area (Osinski and Lee, 2005), and at their greatest depth, have a minimum thickness of 48m. The Houghton Formation is composed of dolomitic silts and muds with subordinate fine-grained dolomitic sands (Frisch and Thorsteinsson, 1978; Robertson and Sweeney, 1983; Hickey et al., 1988). The silts and muds are well-bedded on a millimetre-to-centimetre scale, but massive beds of silt and sand are not uncommon (Hickey et al., 1988; Osinski and Lee, 2005). Carbonate nodules, encasing faunal and floral remains, are known from the lowermost part of the formation. NUFV-405 was discovered in the active layer above the permafrost. This layer is well-exposed and

appears to have been highly cryoturbated, jumbling the sediments and obscuring the lateral continuity of the original bedding planes (Northover, 2009). The majority of NUFV-405 was excavated from grey-coloured silt and clay sediments within this active layer.

Revised Diagnosis

Puijila darwini displays the following derived characters distinguishing it from early-diverging musteloids and oligobunines: long postorbital constriction, anterior palatine foramina placed well anterior to maxillary-palatine suture, enlargement of infraorbital foramen, reduction of post-glenoid foramen, large posterior lacerate foramen, round window larger than oval window, medially-placed and shelf-like P⁴ protocone, reduction of molars, loss of M¹ hypocone, reduction of M¹ postprotocrista, reduction and lingual displacement of M², loss of I₁, posterior displacement of M₁ metaconid, enlarged cervicospinal branch of atlas, reduction of canal for posterior transverse foramina of axis, lesser tuberosity of humerus cylindrical, increased condylar angle of femur, presence of articularis genus fossa on femur, shallow trochlear groove of astragalus.

Puijila darwini differs from *Enaliarctos* and other later-diverging pinnipedimorphs in its possession of a prominent P⁴ parastyle, retention of M¹ pre- and post-protocristae, less reduced molars, less posteriorly displaced M₁ metaconid, retention of distinction between trigonid and talonid of M₁, tympanohyal depression in common pit with stylomastoid foramen, cranial nerves VII and VIII exit the internal acoustic meatus through a common opening, angular process of mandible is not medially deflected, longer humerus-ulna and femur-tibia, presence of entepicondylar foramen of humerus, lack of

cartilaginous extensions of unguals, less reduced ilium, lack of entepicondylar ridge of femur, lack of posterior astragalar process, flat rather than conical patella, unreduced tail.

In contrast to *Potamotherium*, *Puijila* possesses a dorsally arched palate, a well-developed midline palatine ridge, a dorsally-inclined zygomatic arch, an alisphenoid canal, a posteriorly-broader basioccipital, y-shaped basioccipital crest separating ventrally-deep fossae, prominent basioccipital tubercles, an inflated auditory bulla, and an anterior interbullar septum. In addition, *Puijila* lacks antorbital processes, an I₁, accessory cusps of the P₃, an elevated deltopectoral crest, and a shortened, flattened femur.

Comparative Description

Skull

Most of the dorsal portion of the skull is not preserved. The remains of the skull are irreparably fractured into front and back halves at about the mid-length of the skull along a transverse plane. Figure 1.3 and Figure 1.4 displays reconstructions of the skull in various views. Figure 1.5 displays a digital reconstruction and illustration of the skull in ventral aspect, the only view that is not obscured by matrix. No sutures are observed on the skull, even with access to CT imagery.

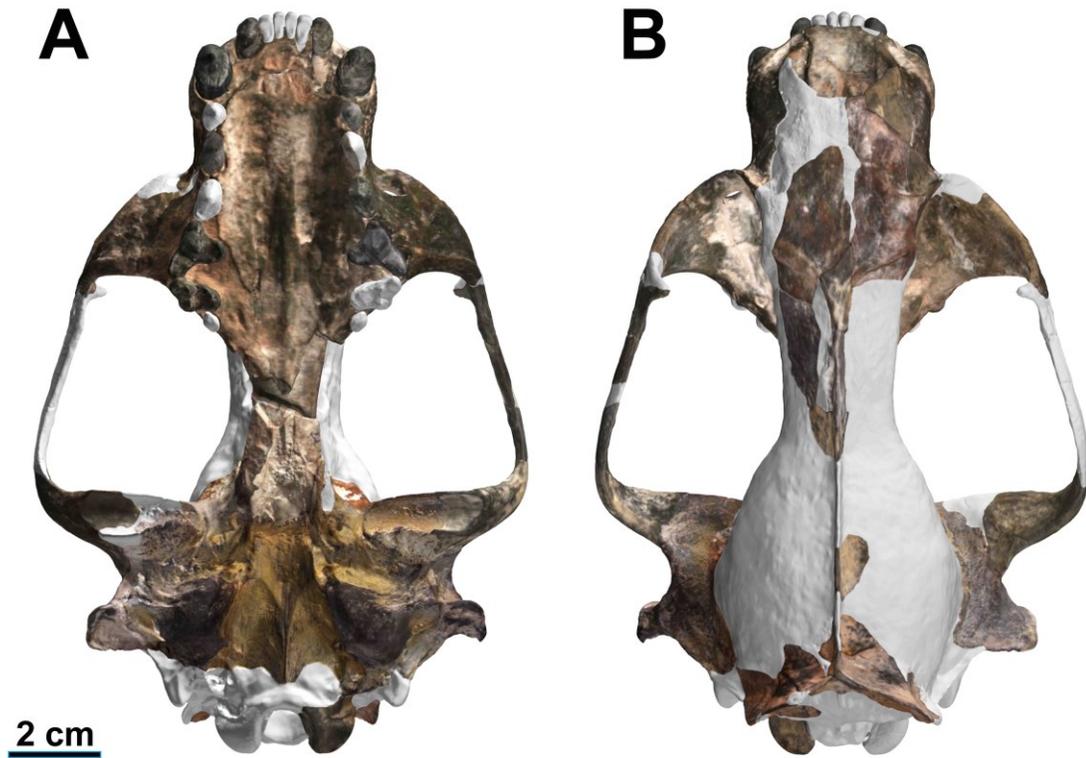


Figure 1.3. Reconstructed skull of *Puijila darwini* in ventral (A), and dorsal (B) views. Grey portions represent reconstructed areas. Images were reconstructed from a surface scan.

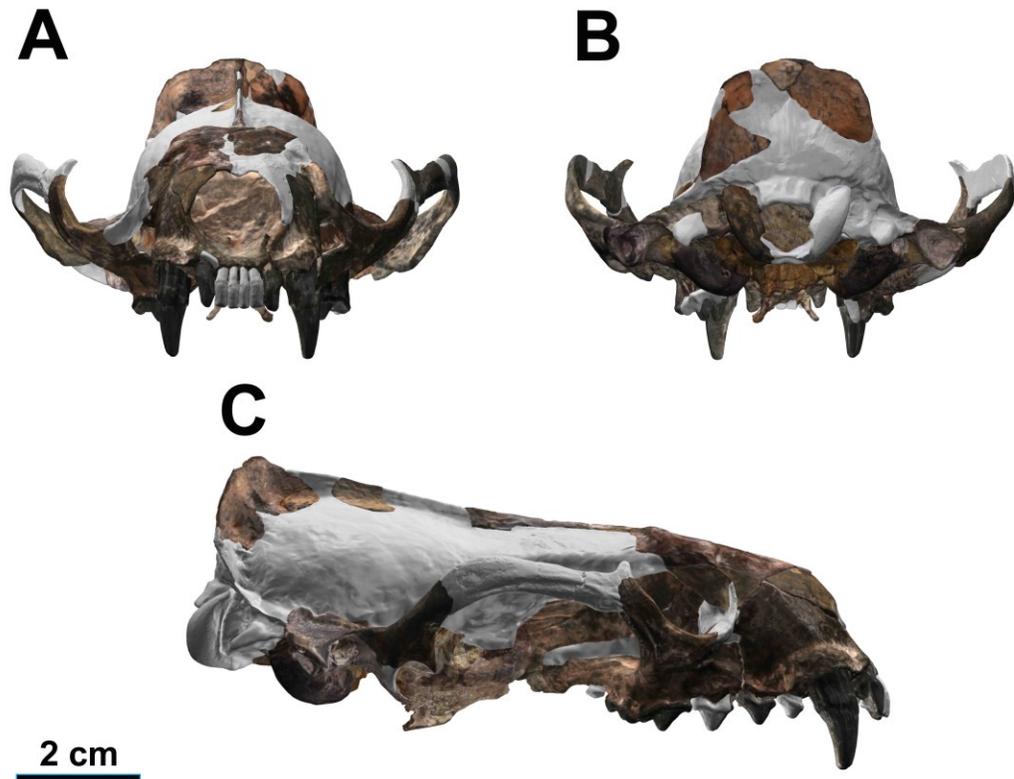


Figure 1.4. Reconstructed skull of *Puijila darwini* in anterior (A), and posterior (B) and lateral (C) views. Grey portions represent reconstructed areas. Images were reconstructed from a surface scan.

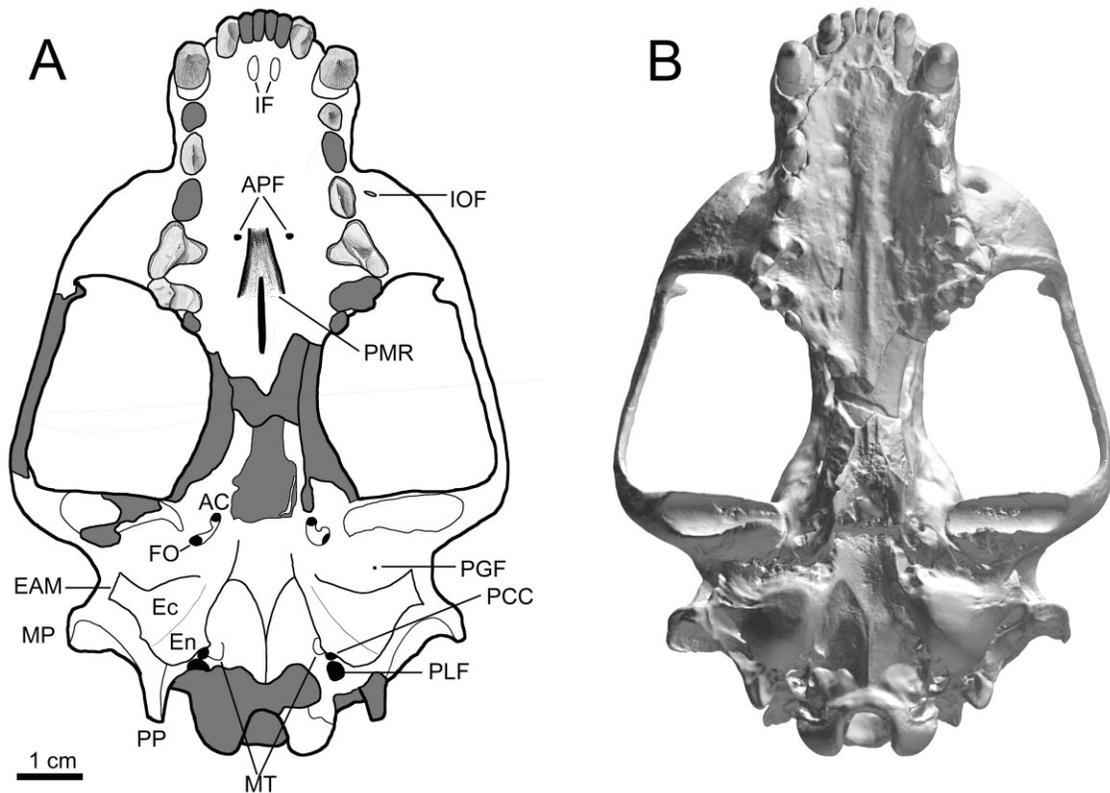


Figure 1.5. Skull of *Puijila darwini* (NUFV-405) in ventral view a=reconstructed surface scan, b=drawing. AC=alisphenoid canal, APF=anterior palatine foramina, EAM=external auditory meatus, Ec=ectotympanic portion of tympanic bulla, En=entotympanic portion of tympanic bulla, FO=foramen ovale, IF=incisive foramina, IOF=infraorbital foramen, MP=mastoid process, MT=muscular tubercles, PCC=posterior opening of carotid canal, PFG=post-glenoid foramen, PLF=posterior lacerate foramen, PMR=palatal midline ridge, PP=paroccipital process.

Facial Portion

The snout is partially fractured along the likely location of the maxillary-premaxillary suture. Anteriorly, the rostrum is thick. Only fragments of the nasal bones are preserved. The most striking aspect of *Puijila*'s snout is the high rostrum.

The ascending rami of the premaxilla are less steep than those of *Lontra* (river otter) or *Potamotherium*. The bone forming the alveolus for the canine is considerably thickened, resulting in a deeply pitted area between the labial aspect of the alveolus and the nasal opening. Medial to this concavity is a raised lateral margin of the nasal aperture. The nasal aperture is bounded laterally by the nasal process of the premaxilla, and ventrally by the palatine process of the premaxilla. It can not be determined if the nasal processes of the premaxilla contact the frontal, as the anterior terminus of the frontal is not preserved.

The infraorbital foramen (IOF) is round and large, though smaller than that of *Lontra*. It is only visible as a slit in dorsal view, and is not at all visible in ventral view. The IOF of *Puijila* differs from that of *Lontra* in being less posteriorly-extensive and more erect, thereby approaching the pinniped condition. The infraorbital canal of *Puijila* is remarkably short (~1mm). Between the canine and the IOF, the maxilla is shallowly concave, possibly representing the caninus fossa of Bininda-Emonds and Russell (1996).

The palatine forms the anterior portion of the palate. Its dorsal surface is rugose, displaying openings for the palatine fissure situated well posteriorly, compared to the openings in *Lontra*. The palatine fissure appears quite large and posteriorly extending as it travels to the nares. The incisive foramina are well-separated from each other, unlike the condition in some species of *Enaliarctos* and some other pinnipeds, in which the foramina are confluent or separated by just a thin flange. The maxillary-palatine suture is completely obliterated, masking its location. A median palatine suture exists on a raised ridge along the midline of the palatine. The maxillary portion of this ridge is about 0.5 cm wide. The ridge expands and becomes less prominent until the anterior border of P⁴. At

this point, the lateral edges of the ridge become indistinguishable from the rest of the palate, but a sharper, more constricted median ridge arises, appearing to continue the length of the palatine. The configuration of this ridge-complex is unique to *Puijila*, but is most closely approximated by *Amphicticeps*, which displays a very similar anterior ridge but lacks the posterior extremity. Correspondingly, a midline groove exists on the dorsal surface of the maxilla and palatine of NUFV-405 (visible in HR μ CT data). The degree of concavity of this groove nearly approximates the degree of convexity of the ventral midline ridge.

The paired major (anterior) palatine foramina are small, and aligned with the anterior border of P⁴, adjacent to the raised ridge of the median palatine suture. They are continuous with the elongated palatine sulci, which run anteroposteriorly along the length of the palate. Like *Potamotherium*, the anterior palatine foramina are located well anteriorly, though their precise location relative to the maxillary-palatine suture is unknown. The medial portion of the ventral surface of the palate is strongly dorsally-arched, reaching an apex between P³ and P⁴.

The orbit appears very large. The left lacrimal is likely present, preserving a lacrimal foramen just posterior to the vestigial antorbital process, but the actual sutures of the lacrimal cannot be discerned. The antorbital rim extends dorsally to the vestigial supraorbital process, and is separated from the rostrum by the nasolabialis fossa. Unlike the condition observed in extant pinnipeds, this nasolabialis fossa is not restricted to the rostrum, but also extends laterally onto a thin dorso-ventrally elongated flange.

Ventral to the orbit, the maxilla flares laterally to contact the jugal. This portion of the maxilla is somewhat concave ventrally, owing to raised ridges present at the posterior

orbital margin and the anterior margin of the temporal fenestra. The jugal appears to form the ventral part of the orbit, as a fracture exists along a potential maxillary-jugal suture, but confirmation of this suture is not possible, even with CT images. Fragments of the nares and frontals appear dorsally high, and the post-orbital constriction appears significant and extensive, though conclusive remarks are not possible as the dorsal portion (=skull roof) is mostly not preserved.

The zygomatic arch is almost entirely preserved on the left side. The dorsally extending post-orbital process of the jugal is fragmentary, but appears long, and is inclined somewhat medially. The jugal and squamosal appear to interlock on an anteroposteriorly straight zygomatic arch.

The parasphenoid becomes mediolaterally compressed, as does the palatine, posteriorly. The palate is posteriorly expanded, extending well beyond the posterior margin of the M², though its posterior terminus is not preserved. The maxilla also continues posteriorly around the lateral border of the palatine. It does not begin to constrict until after the M², and a portion still stretches laterally beyond the skull past the M².

In coronal view, the choana are relatively rounder than those of *Canis*, most closely resembling those of *Enhydra*. The lateral walls of the choana are somewhat rounded. The dorsal wall of the choana is less flat than the ventral wall, and comes to an apex at the midline, at the location of the vomeral crest. At its most ventral extent, the crest of the vomer projects about a third of the way into the choana. At this point, roughly where the median palatine ridge terminates, the vomeral crest is flange-like, before shortening and becoming slightly more bulbous posteriorly.

Parietal Region

Fragments of the sagittal crest are present and have been reassembled. Anteriorly, the temporal crests begin just posterior to the orbits. Paired prominences travel medially and somewhat posteriorly from the supraorbital processes, converging into a posteriorly directed ridge on the midline, which quickly sharpens into a sagittal crest. These prominences travel less obliquely than those in *Enaliarctos tedfordi* and *Enaliarctos barnesi*, and somewhat resemble the more laterally-oriented transverse prominences observed in *Pacificotaria*. The sagittal crest is very sharp and high, producing deep concavities laterally. The crest continues to the posterior margin of the skull where it diverges into an equally sharp lambdoidal crest, which produces another concavity on the posterior surface. The lambdoidal crest of *Puijila* extends latero-posteriorly for a brief length, before dropping off at almost a vertical plane and curving anteroventrally to meet the zygomatic. The lambdoidal crest of *Puijila* completely obscures the occipital region in dorsal view, whereas in *Enaliarctos* and some later-diverging pinnipeds the occipital region is well-exposed in dorsal view.

Occipital Region

Basioccipital

The basioccipital appears trapezoidal. Its ventral surface becomes mediolaterally-expanded posteriorly. This expansion causes the tympanic bullae to orient obliquely. The muscular attachment sites for the origin of the longus and rectus capitis muscles lie prominently against the medial surfaces of the bullae, appearing as ridges barely, but visibly distinct from the margin of the bullae. Posteriorly, these flanges terminate in

knob-like processes that protrude medially. These pharyngeal processes (or muscular tubercles), extend medially from the medial entotympanic wall of the auditory bulla, and are accompanied by a thickening of the portion of the entotympanic from which they are derived. They may represent additional attachment sites for the rectus capitis. Similar tubercles are present and variably prominent in many early arctoids, though those of *Puijila* most closely resemble those observed in *Paragale*, differing only in size - those of *Puijila* are larger and more prominent. Anteriorly, the ridges continue before gradually vanishing into the basisphenoid, near the posterior-most extension of the pterygoid. A sharp keel runs along the mid-length of the posterior portion of the basioccipital. Anteriorly, this keel diverges into a pair of obliquely-oriented, less well-developed crests that connect to the muscular tubercles and also likely serve as capitis muscle attachment sites. This Y-shaped basioccipital cresting is observed in many canids, ursids, and early pinniped ancestors, but is absent in mustelids, except for *Gulo* (wolverine). Enclosed between these crests and the lateral edges of the basioccipital are hemispherical fossae with triangular anterior portions. These fossae are heavily canted from the midline, displaying significant posterolateral excavation for the rectus capitis ventralis. Beyond these fossae, the anterior portion of the basioccipital is slightly concave. The posterior carotid foramina, lying lateral to the knob-like processes, are embedded within the posteromedial border of the bullae, and open 45 degrees from the midline. The posterior carotid foramina are barely visible in ventral view. Posteriorly, in very close proximity to the posterior carotid foramen but not confluent with it, lies a large, round posterior lacerate foramen opening at a slightly oblique angle. Hypoglossal foramina are not preserved in this specimen.

The lateral margins of the basioccipitals are deeply embayed to house the inferior petrosal sinuses, only visible in the CT data (Figure 1.6). The tract for the inferior petrosal sinus begins toward the anterior origin of the bulla, where the posterior clinoid processes decrease in height and migrate laterally, and continues posteriorly until the bullae themselves recede and the ventral excavations of the basioccipital exert themselves. A long, thin dorsal arm extends to the petrosal, completely roofing the embayment for most of its length. Like that of *Enaliarctos emlongi*, the petrosal of *Puijila* is medially excavated to further accommodate the large canal. The canal is floored ventrally by the basioccipital, and is thus completely enclosed for much of its length. The inferior petrosal sinus never appears to communicate directly with the carotid canal, but the two are separated by just a thin bony lamina. The embayments are over half the height of the bullae, and well over twice the height and width of the carotid canals. The carotid canal runs along the medial portion of the auditory bulla. The carotid canal rises dorsally as it enters the skull, before ultimately falling ventrally again as it exits through the posterior carotid foramen, all the while shifting slightly laterally in line with the lateral displacement of the bulla, associated with the posteriorly expanding basioccipital.

Anterior to the basioccipital is an anteriorly tapering basisphenoid. The basioccipital and basisphenoid are well-fused with each other, making inferences on the position of the suture difficult. The basisphenoid appears shallowly concave. Only the posterior portion of the basisphenoid is externally visible. The remainder is obscured by a natural endocast of the pterygoid region. The ventral surface of the basisphenoid is concave, and confluent with the basioccipital.

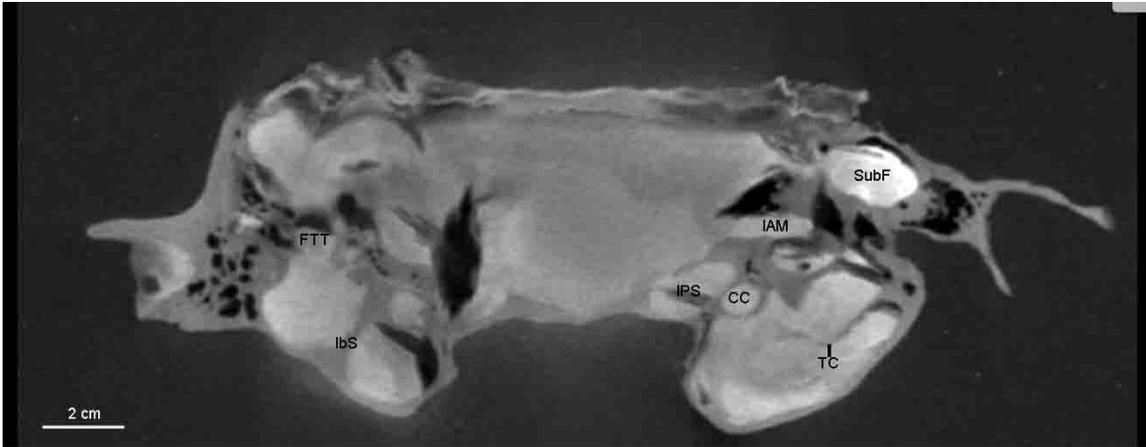


Figure 1.6. A coronal slice of *Puijila darwini* (NUFV-405) taken from the HR μ CT data displaying extent of the inferior petrosal sinus. CC=carotid canal, FTT=fossa for the tensor tympani, IAM=internal acoustic meatus, IbS=intrabullar septum, IPS=inferior petrosal sinus, SubF=subarcuate fossa, TC=tympanic crest.

The tympanic bullae are completely ossified. In ventral view, they are bulbous and slightly longer than wide. They are oriented at an oblique angle. A slight keel begins at the anteromedial border as a small process and runs along the apex of the bulla parallel with its medial border, vanishing about halfway across the bulla's length. This keel likely distinguishes the ectotympanic from the entotympanic. Laterally, the bullae are anteroposteriorly and dorsoventrally constricted into a long, cylindrical extension of the ectotympanic. This tubular trough of the ectotympanic opens laterally into a circular external auditory meatus, and connects posterolaterally to another smaller ridge representing the anterior flank of a large mastoid process. On the dorsal surface of the external auditory meatus is a shallow and anteroposteriorly-short suprameatal fossa (Figure 1.7). A low septum (=ectotympanic pseudoseptum) is present within the anterior portion of the bulla, similar to that observed in *Enaliarctos mealsi* and *Enaliarctos emongi*. It crosses posterolaterally from the ventromedial wall of the carotid canal to a

point on the ectotympanic, lateral to the probable entotympanic/ectotympanic suture. The tympanic crest (=crista tympanica), which supports the tympanic membrane, is of a very narrow anteroposterior diameter, but is very flange-like, and protrudes well medially into the tympanic cavity, similar to the condition in *Enaliarctos mealsi* and *Enaliarctos emlongi*. A pair of small foramina, the anterior carotid foramen and the median lacerate foramen, are located the the anteromedial border of the bulla. These foramina share a common opening, though a slight crest is externally visible, continuous with their internal partition. Lateral to the anterior origin of the crest is the anterior carotid foramen. Dorsal and slightly lateral to the anterior carotid foramen is a slightly larger opening, for the foramen lacerum (median lacerate foramen), which opens medially into the cranial cavity.

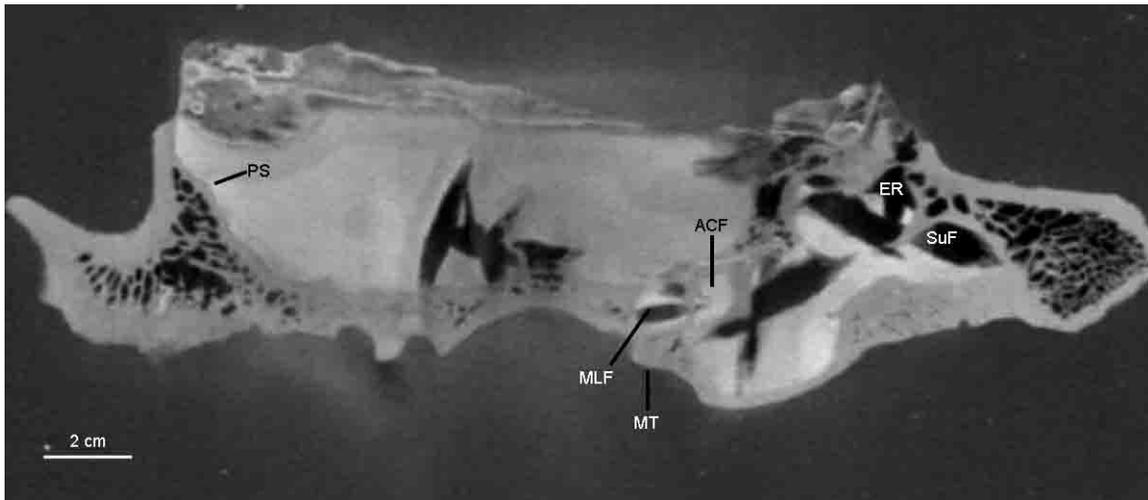


Figure 1.7. A coronal slice of *Puijila darwini* (NUFV-405) taken from the HR μ CT data displaying displaying shallow suprameatal fossa and deep epitympanic recess. ACF=anterior carotid foramen, ER=epitympanic recess, MLF=median lacerate foramen, MT=muscular tubercle, PS=pseudosylvian sulcus, SuF=suprameatal fossa.

The petrosal is only visible in the CT-data, and some of its features are obscured by inclusions of matrix. The perimeter of the dorsal portion of the petrosal is difficult to

identify, but it appears as if the dorsal portion of the petrosal is relatively unexpanded, though somewhat inflated. The petrosal apex is not sharply pointed, resembling the condition observed in otariids and desmatophocines. The internal auditory meatus is dorsoventrally wide, and appears to be a confluence of the two cranial nerves separated internally by a small medially-projecting flange of bone at the level of the opening. This resembles the condition in *Enaliarctos emlongi*, though the prong-like embayments surrounding the flange appear less extensive than in *Enaliarctos*, indicating the state in *Puijila* is likely transitional between terrestrial taxa and later-diverging pinnipedimorphs. However, matrix inclusion in this area precludes certain determination of this feature. An oval window opens primarily laterally. The round window is nearly twice the diameter of the oval window, and opens primarily posteriorly, though it is also somewhat visible in dorsal and lateral views. A shallow crater surrounds the round window, possibly representing the round window fossula of Wyss (1987). Anterior to the oval window, a well-rounded fossa for the tensor tympani is carved into the lateral wall of the promontory (Figure 1.6). Posteriorly, as the fossa for the tensor tympani recedes, the epitympanic recess opens just lateral to it. The epitympanic recess is broad and well-excavated dorsally into the temporal bone, reaching well beyond the dorsal limit of the fossa for the tensor tympani (Figures 6 and 7). Posteriorly, the epitympanic recess becomes enclosed by its own dorsomedially-outstretched lateral wall, and quickly fades into a fossa. No mastoid sinus is present. No posterior promontorium process is present. The subarcuate fossa (=cerebellar fossa) begins just posteriorly to the petrosal apex (Figure 1.6). The subarcuate fossa is large and round, and about twice the diameter of the carotid canal.

The mastoid process is significantly laterally expanded and somewhat ventrally expanded, with a concave posterior surface. The concavity is amplified due to its enclosure by a thickened ridge, marking the lateral, ventro-anterior, and ventro-medial margins of the mastoid process. Medially the ridge tapers to a low keel, that may connect postero-medially to an unpreserved paroccipital process. Between the mastoid process and the bulla lies a large stylomastoid foramen. Posteromedially to the stylomastoid foramen is a smaller tympanohyal pit (hyoid fossa). Between the two lies a small flange-like protuberance extending from the lateral wall of the bulla. Exaggeration of this development is observed in the enaliarctids and otariids, in which this process becomes a thin flange completely separating the two openings.

The large mediolaterally-expanded and tubular extension of the ectotympanic does not directly appress the glenoid. A vestigial retroarticular foramen (post-glenoid foramen) is observed medial to the junction between the retroarticular process and the ectotympanic (Figure 1.7). The reduction of this foramen is also observed in *Enaliarctos* and *Potamotherium* (Mitchell and Tedford, 1973) and is believed to reflect an aquatic adaptation for internal jugular drainage. The retroarticular (postglenoid) process is large, more so medially, and broader than that of *Lontra*. The mandibular fossa of the glenoid is long and narrow, corresponding to the cylindrical articular condyles of the mandible. The preglenoid process is present, though reduced compared to the post-glenoid process, and is short medially and somewhat higher laterally (similar to *Pacificotaria*).

Medial to the glenoid is the foramen ovale. The foramen ovale opens anteroventrally and shares a common fossa with the caudal alar foramen, which sits anteromedially and opens lateroventrally, penetrating the alisphenoid strut. Medial to

these foramina, a concave, obliquely oriented ridge, encasing the alar canal, runs anteroventromedially towards the pterygoid, along the length of the medial portion of the alisphenoid. This contrasts with the mustelid condition of a distinctive keel-like medial wall of the alisphenoid along this length. NUFV-405 preserves a posterior process of the alisphenoid. Anteriorly, the alisphenoid continues, but is only represented by a robust cylindrical endocast. The humulus of the pterygoid is well-preserved, but somewhat obscured by matrix. The humulus is relatively flattened and somewhat broad. It is raised well above the basisphenoid (1.2 cm).

Inspection of CT data reveals the optic canal, orbital fissure and rostral alar foramen share a common opening anteriorly (Figure 1.8). This shared canal is anteroposteriorly extensive and wider than tall. Almost immediately after the opening, the mediolaterally broadened optic canal, enclosed dorsally by just a thin flange of bone, departs for the cranial cavity. Travelling posteriorly, the orbital fissure migrates dorsally, opening abruptly into the endocranial space. The posterior extension of the alar canal is slightly smaller and longer than the posterior extension of the orbital fissure, finally ending at about the level of the post-glenoid process.

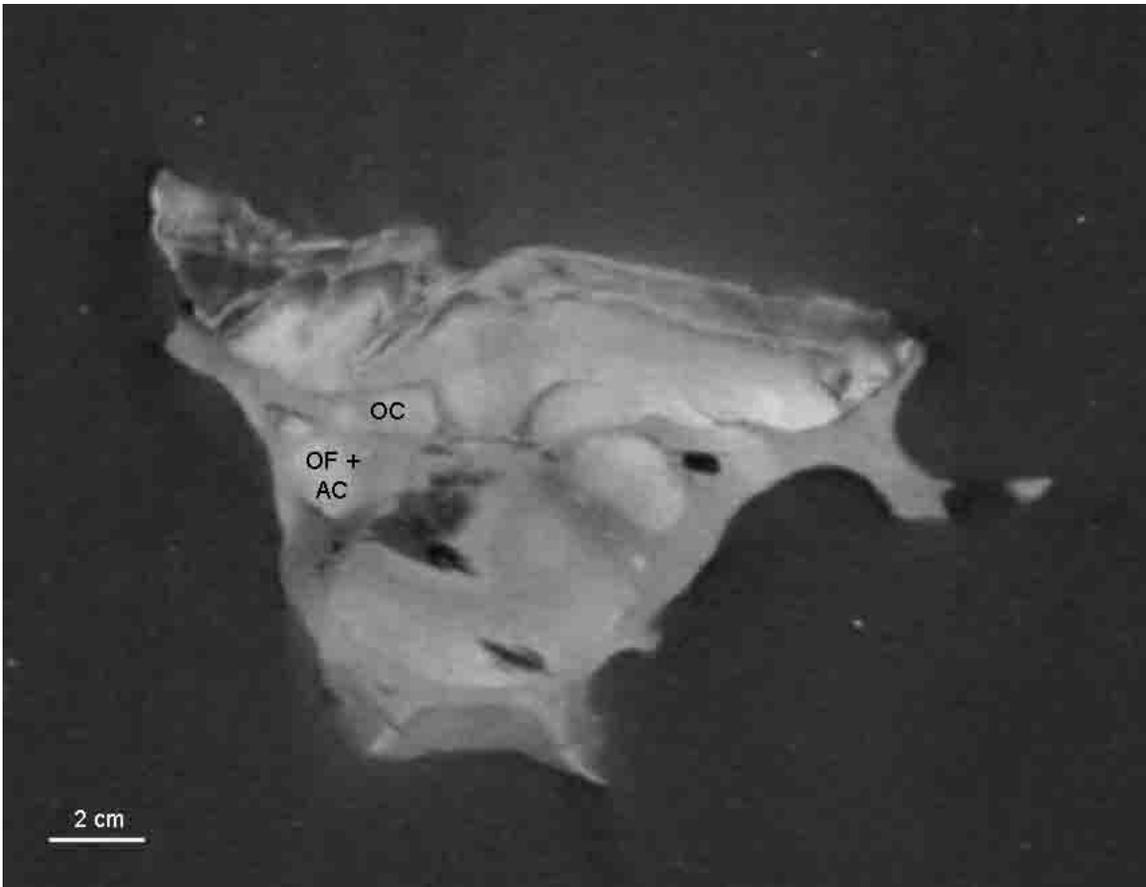


Figure 1.8. A coronal slice of *Puijila darwini* (NUFV-405) taken from the HR μ CT data displaying confluence of optic canal, orbital fissure, and rostral alar foramen. AC=alisphenoid Canal, OC=optic Canal, OF=orbital fissure.

Dorsal to the mastoid process, the squamosal is concave and appears laterally extensive. Anteriorly, the dorsal surface of the squamosal becomes convex and narrows, before again becoming shallowly concave, and flaring laterally as it contributes to the zygomatic arch. This concavity is confluent with a wide groove present on the lateral wall of the cranium. While this area is not well-preserved, the external braincase morphology can be further inferred from the matrix-filled endocast, which reveals that this groove continues dorsally.

Dorsally the squamosal sulcus appears confluent with a rudimentary pseudosylvian sulcus on the lateral wall of the braincase. The pseudosylvian sulcus is better visible in the CT images, though only its ventral portion is discernable (Figure 1.7). This sulcus is so strongly developed in *Potamotherium* and other pinnipedimorphs that it is immediately evident on the external surface of the braincase. Certain identification of this feature in *Puijila* should await more complete material.

The zygomatic process of the squamosal is quite thick - thicker than that of *Lontra* - and appears to arch dorsolaterally, contributing to a dorsally high zygomatic arch, similar to *Potamotherium* and *Ailurus*.

An endocast of the bony labyrinth has been segmented out (Figure 1.9), allowing for appraisal of the semicircular canals and cochlea. In appearance, the semi-circular canals share a resemblance to those of semi-aquatic musteloids (Grohé et al., 2016), displaying an enlarged, sinuous lateral canal that shares an acute angle with the posterior canal. However, they also depart from the lutrine condition by possessing well-rounded canals, rather than elliptical canals, and a ventrally-directed cochlea. The posterior ampulla is robust. The cochlea is oriented more transversely than that of any other non-phocid arctoid depicted in the literature (Ekdale, 2013; Grohé, 2016).

The left occipital condyle is preserved in isolation. It is similar in size and shape to that of *Lontra*. Whereas the occipital condyle of *Lontra* continues to expand anterolaterally, the occipital condyle of *Puijila* is thickest centrally, narrowing towards its edges. The occipital condyle appears to protrude well beyond the sagittal crest. A canal is present on the medial surface within the foramen magnum, opening at about the mid-width of the condyle just medial to it (hypoglossal foramen). In *Lontra*, this foramen is

larger and slightly more medially positioned. The ventral edge of *Puijila*'s occipital condyle turns sharply medially. The orientation of the ventral and dorsal edges indicates the occipital condyle was more vertically erect than that of *Lontra*.

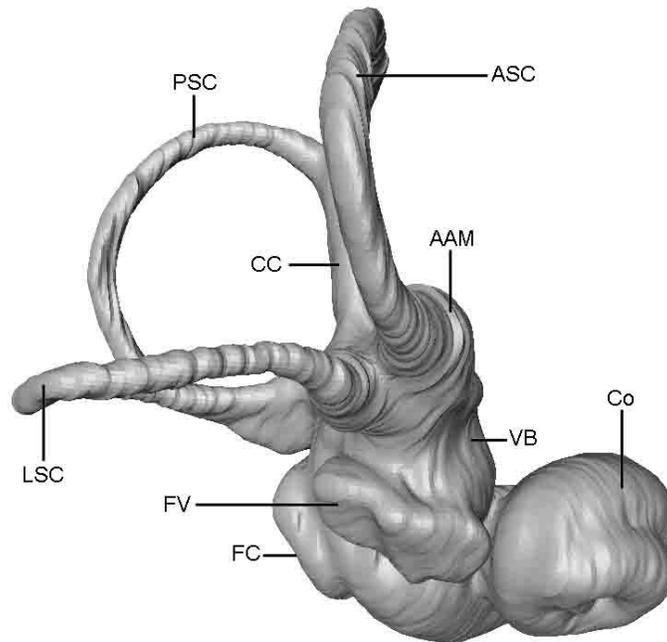


Figure 1.9. Digitally segmented endocast of right bony labyrinth of NUFV-405 in anterolateral view.

AAM=anterior ampulla, ASC=anterior semicircular canal, CC=common crus, Co=cochlea, FC=fenestra cochleae, FV=fenestra vestibule, LSC=lateral semicircular canal, PSC=posterior semicircular canal, VB=vestibule.

Mandible

The left and right mandibles are nearly complete (Figure 1.10). Only the antero-dorsal portions of the ramus are fragmentary. The mandible is quite thin mediolaterally. The mandibles are not ankylosed, and the symphyseal regions are deeply sculptured. The symphyseal areas are ovoid and slightly expanded ventrally, producing a slight ventrally-

extending symphyseal boss visible in lateral view. The symphyseal boss is not nearly as

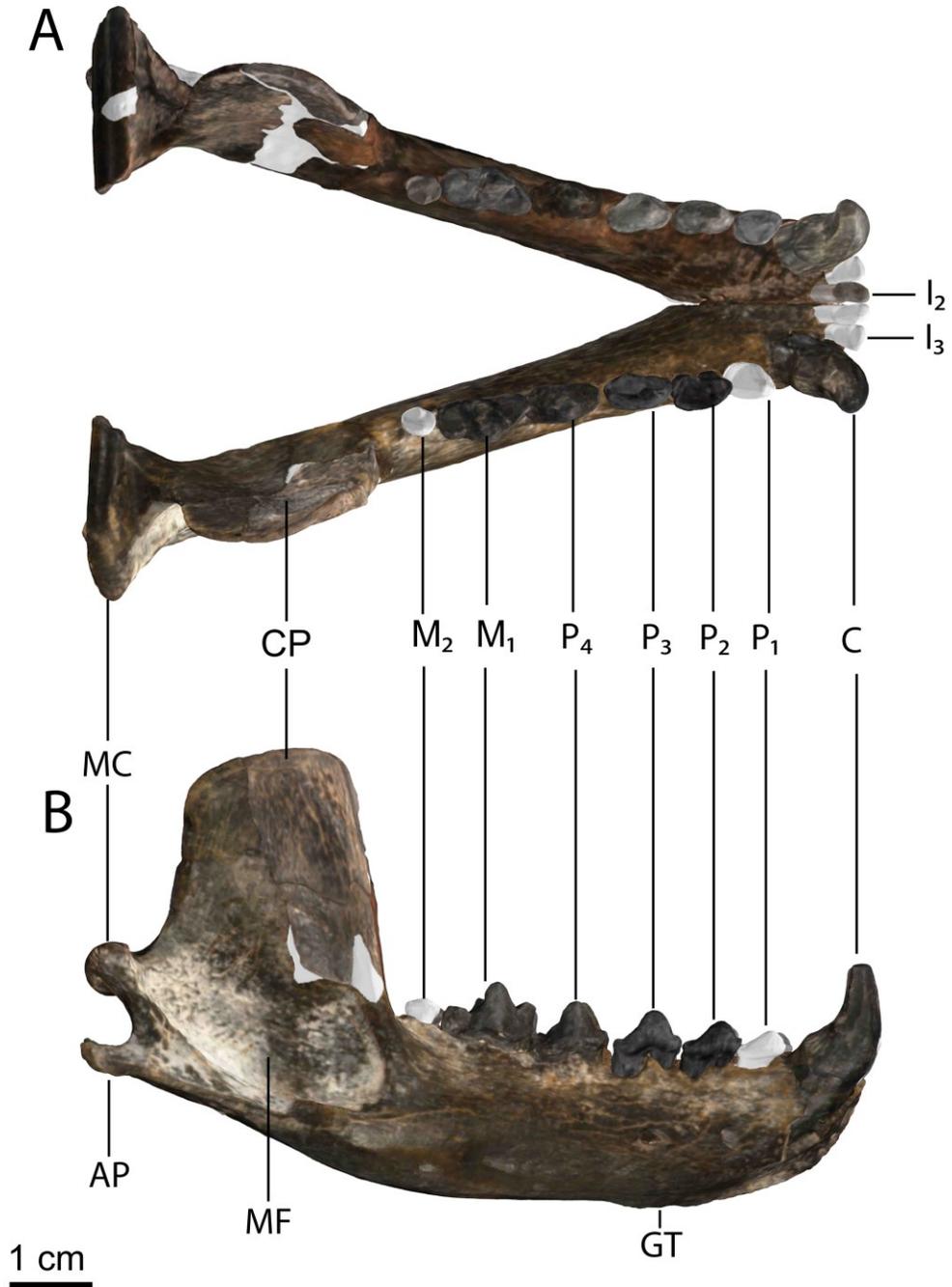


Figure 1.10. Mandible of NUFV-405 in occlusal (A) and lateral (B) views. Grey=Reconstruction.

AP=angular process, C=lower canine, CP=coronoid process, GT=gluteal tuberosity,

MC=mandibular condyle, MF=masseteric fossa.

well developed as that of *Kolponomos*, but more ventrally extending than that of *Lontra*, most closely approximating *Potamotherium miocenicum* in its degree of development. The horizontal ramus is deepest at this boss and becomes progressively more shallow posteriorly as it curves gently in a dorsal direction. This contrasts with *Lontra*, which exhibits a distinct masseteric line on a different plane that is still parallel with the rest of the ventral margin. Ventrally, the posterior portion of the ventral border is flattened, unlike the rounded ventral border of *Lontra*. The horizontal ramus is dorsoventrally expanded compared to similarly-sized mustelids.

The alveoli for the incisors are not in line with each other. The alveolus of I₁ is posteromedial to the alveolus of I₂. Anteroventrally, paired foramina lie immediately ventral to the alveolar openings of the incisors. Laterally, two mental foramina lie at the mid-depth of each mandible. The more anterior of the two lies beneath the anterior border of M₁, partly on a slight depression at the mid-depth of the mandible extending to the posterior border of P₁. This depression separates the raised cylindrical alveoli for the root of the enlarged canine from the rest of the mandible. The more posterior of the two mental foramina lies beneath the anterior half of P₃.

The masseteric fossa is deep (0.69 cm from deepest recess to highest edge of the fossa – the coronoid crest). The coronoid crest sits on the anterior border of the ascending ramus and is much thicker than the rest of the ascending ramus. Ventrally, the coronoid crest meets the anterior extension of the masseteric crest. Posteriorly, the masseteric crest diverges into a pair of crests encasing a 0.5 cm wide ridge. The more ventral of the two extends to the thin, elongated, hooked, angular process. Ventrally, the angular process is flat. The angular process is slightly laterally offset from the long axis of the tooth row

and located dorsal to the ventral margin but ventral to the tooth row. A ridge exists on the dorsal side of the angular process, separating small pits on either side – all are likely attachments of the internal pterygoid muscle. The angular process projects posteriorly, causing the condyloid notch to appear semi-circular. Dorsal to the angular process and separated from it by a notch is the condyloid process (or articular process). The articular process is cylindrical, pointed laterally, and deepest medially. At the anteromedial base of the condyle lies a barely visible insertion pit for the external pterygoid (Tedford, 1994), while the lateral border serves as an attachment for the masseter. The articular condyle is slightly dorsal to the plane of the tooth row, as observed in *Enaliarctos*. The articular process is separated from the coronoid process by a mandibular notch deeper than that of *Lontra*.

The medial surface of the ascending ramus has a narrow, but salient ridge roughly in line with the tooth row for attachment of the temporal muscles. Below the mid-length of this ridge lies a mandibular foramen. Unlike *Lontra*, the mandibular foramen is separated from the temporal muscle attachment by a few millimetres. The ascending ramus itself is roughly rectangular with rounded edges. The coronoid crest is deflected slightly posteriorly (roughly 110 degrees from the tooth row).

Upper Dentition

Only two alveoli are externally visible for the upper incisors, for the second and third incisors, respectively. HR μ CT scans show a small, shallow alveolar opening on each side for I¹ (Figure 1.11). However, this alveolus lacks a root and is nearly completely obliterated. It is possible the adult I¹ never emerged.

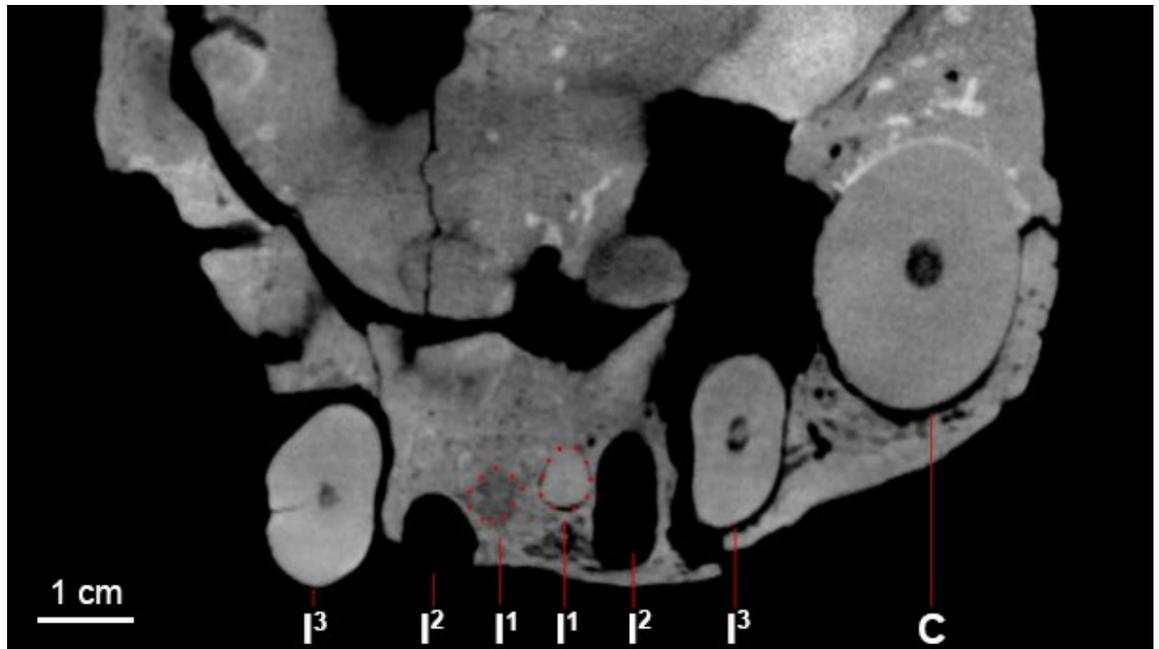


Figure 1.11. Transverse slice from HRμCT data displaying alveolus of first incisor in NUFV-405.

I¹=first incisor, I²=second incisor, I³=third incisor, C=canine.

The I³ is the only incisor preserved on this specimen, and it is preserved on both sides. The I³ is asymmetrical, being highest medially, at a pointed cusp, before sloping down to the latero-posterior margin, where a cingulum is present. The I³ is procumbent, protruding well past the rostrum. The alveolar opening for the I² is much smaller than the I³ alveolus. The three alveoli are all aligned with each other, and separated from the canine by a small diastema.

The canine is very large. The crown is nearly round in cross-section, slightly curved medially, and heavily curved posteriorly. A prominent cingulum girdles the base of the crown, and is most prominent lingually. Fluting is visible ventral to the cingulum.

Closely appressed to the canine is a small, single-cusped P₁ with a moderate amount of bucco-distal cingulum. The P² is also single-cusped but two-rooted, and

somewhat buccal-lingually compressed. Its basal cingulum is prominent, particularly lingually. The crown of its posterior root is inferior compared to the anterior root's crown. Like the P², the P³ is two-rooted. The P³ displays a primary cusp that slopes posteriorly to meet an accessory cusp

P⁴ is three-rooted, and the largest of the upper post-canines by a considerable margin. The mesio-buccal corner displays a low parastyle, rising barely above the level of the buccal cingulum. Buccally, the parastyle is confluent with strong cingulum. Lingually, the cingulum is discontinuous. Distally, a groove separates the parastyle from the interior, where a ridge sweeps up to meet a high paracone. The trenchant paracone is separated from a lower, disto-buccally located metacone by a narrow carnassial notch. The metacone is mesio-distally elongated and connects with a high metastyle. This metastyle is less elongated than most specimens of *Potamotherium*, approaching, but not reaching, the level of reduction observed in *Enaliarctos mealsi*. In many specimens of *Potamotherium*, the metastyle flares laterally beyond the parastyle of the M¹, a feature not observed in NUFV-405. The lingual portion of P⁴ is deep and rounded in occlusal aspect with a prominent basal cingulum surrounding a low, shelf-like protocone. This protoconal shelf shares a coronal plane with the paracone, rather than being situated anterior to it, and terminates just mesial to the carnassial notch. The protoconal shelf of *Potamotherium* is anteroposteriorly broader, as its distal border extends to contact the labial portion of the tooth well past the level of the carnassial notch. Running posteriorly, the crown of NUFV-405's P⁴ slopes up considerably, further exaggerating the in-situ height of the metastyle. The long axis of P⁴ is oblique, nearly 45 degrees from the sagittal

plane. Between the P⁴ and the M¹ is a shallow embrasure pit, similar to that of *Enaliarctos barnesi* and *Enaliarctos mitchelli*.

M¹ is a three-rooted tooth. Its long axis runs mediolaterally. The M¹ is broad laterally and narrow anteroposteriorly, lacking parallel borders. The parastyle is level with and appresses the metacone of P⁴. Lingual to the parastyle and level to it is the paracone, and distal to that is a slightly inferior metacone. The protocone is separated from the paracone and metacone by a wide notch, and barely rises above said notch. A faint postprotocrista runs posterolaterally across the talonid as it approaches, but doesn't reach, the metacone. The appearance of the postprotocrista in NUFV-405 most closely resembles that of *Amphicticeps*. Both taxa displayed a reduced postprotocrista that is angled more posteriorly than laterally. No metaconule is present in NUFV-405.

Prominent cingulum rings the entire base of M¹. Linguodistally to the protocone of the M¹, about 30 degrees to the tooth row, is a small, single-rooted M². It displays a flat crown that is somewhat rounded, and slightly expanded mesio-distally. It houses incipient cusps on the buccal and lingual borders, likely the metacone and protocone, respectively.

Lower Dentition

From the alveolar openings, one may infer a pair of small incisors (I₂ and I₃) were present in each mandible. An isolated I₂ was preserved, and appears to have protruded slightly beyond the anterior mandibular margin. They likely protruded slightly beyond the anterior mandibular margin. The alveolar opening for the I₃ suggests it was situated slightly behind the I₂, and was less erect than the I₂ in lieu of being directed ever-so-

slightly labially. The long-rooted, conical canine is in line with the likely position of the I₂, and slightly anterior to I₃. The crown of the canine is also long, and gently curved posteriorly. A cingulum is present on the disto-lingual border of each canine. Significant fluting is observed just dorsal to the cingulum, more saliently on the posterior side.

The post-canines are all within the same row. The P₁ is mesio-distally compressed, single-rooted, and displays lingual cingulum. The P₂ and P₃ are similar in size and shape to each other, displaying the typical carnivoran morphology. Both are double rooted and single cusped with bucco-distal cingulum. The crowns are posteriorly elongated and their posterior halves are expanded both buccolingually and mesiodistally. The P₃ is slightly larger than the P₂, and exhibits a more erect cusp, in comparison to the more anteriorly-situated and anteriorly-sloping cusp of P₂. The P₄ is double-rooted and multi-cusped, displaying a prominent paraconid, a raised protoconid reaching well above the cusps of P₂/P₃, a gently-projecting metaconid, and a low, broad hypoconid on the distal border. The high-rising protoconid creates a triangular crown in lateral view.

The M₁ is very large and two-rooted with a well-developed trigonid. On the buccal border, at about the mid-length of the tooth, a very large protoconid rises higher than any other cusp of the mandibular dentition. The protoconid is broad, triangular and nearly erect, though slightly sloping posteriorly. Anteriorly, a notch separates it from a blunt paraconid. The paraconid is centrally-positioned at the mesial border of the M₁, and is slightly higher than and larger than the metaconid. The metaconid sits on the lingual border of the tooth, and is slightly more distally-positioned than the protoconid. Together, the metaconid and the protoconid serve as a steep cliff with a nearly erect distal wall overlooking the talonid. Compared to the trigonid, the talonid is small and low – even

lower than the M₂. The talonid slopes inward anteriorly from a vestigial hypoconid to produce a talonid basin. There is prominent cingulum present on the anterior portion of the buccal sides. The cingulum extends to the lingual side, where it is less well-developed.

Posteriorly and ever so slightly lingual in position to the M₁ is a small M₂. The M₂ is sagittally oval and is ringed by a cingulum. The metaconid is the most prominent cusp. A reduced protoconid lies on the buccal side of the tooth, in-line with the metaconid, and trailed anteriorly and posteriorly by a preprotocrista and a postprotocrista, respectively. An incipient paraconid appears to be present on the mesial margin. The rim of the M₂ alveolus is the highest of those in the mandibular dentition.

Axial Skeleton

Atlas

The atlas (Figure 1.12) is similar in shape to those of *Lontra* and *Potamotherium*. Anteriorly, the facets for the occipital condyles are very concave. They are more bowled than those of *Lontra*, due to a medial extension of their dorsal border, just ventral to the circular oblique foramen. The oblique foramen of *Lontra* is sub-ovular. The body and neural arch are not well-preserved, but appear similar in dimensions to those of *Lontra* and *Potamotherium*. Caudally, the caudal articular facets are similar in shape to those of *Lontra*, but extend slightly more caudally, resulting in foveae that are more concave than those of *Lontra*. Lateral to these foveae are the transverse foramina, which display shortened canals, but like *Potamotherium*, have a wider diameter than those of *Lontra*.

The transverse foramina are not visible in dorsal view. The cranial opening of the canal is very wide, present on the transverse process itself rather than at the junction of the transverse process and the lateral wall of the foramen magnum. Through the lateral wall of the transverse foramina runs the cervicospinal canal, which exits on the lateral wall of the vertebral canal through a foramen larger than that of any mustelids examined.

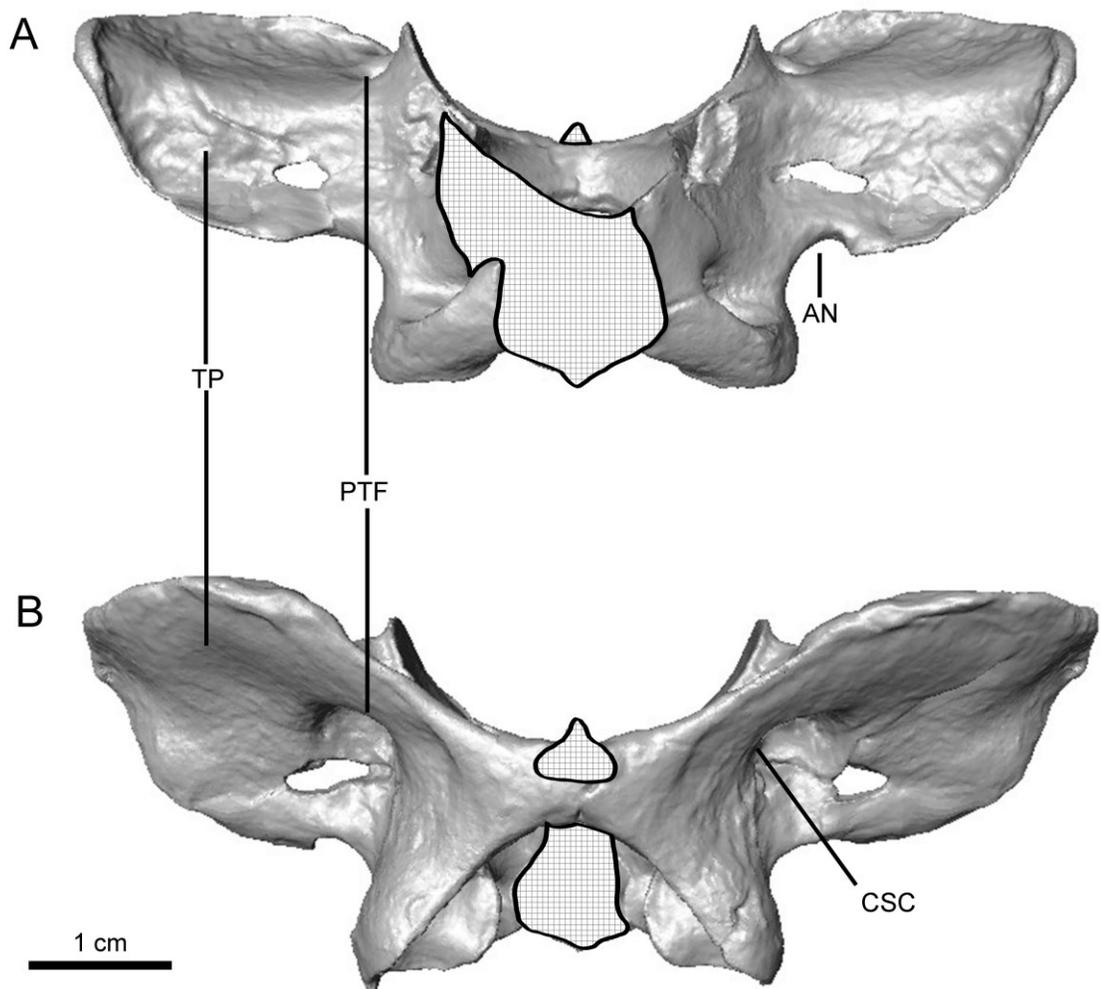


Figure 1.12. Surface scan of atlas of NUFV-405 in dorsal (A) and ventral (B) Views. Gray=Bone. AN=alar notch, CSC=cerebrospinal canal, PTF=posterior transverse foramina, TP=transverse processes. Stipling indicates areas that are not preserved.

The transverse processes are very large with less thickened lateral borders, and more expanded than the condition in *Lontra*. They are not as well-rounded as those of *Potamotherium*. The caudal portion of the transverse process is more ventrally situated than the cranial portion, resulting in a 45-degree angle from the main axes. The alar notch is quite distinctive. Due to the expansion of the transverse processes, the alar notch appears swoosh-shaped.

The ventral surface of the atlas is not uniformly concave, as is observed in *Lontra*. The dorsal surface is convex with shallowly concave edges enclosed by sharply defined borders. The peripheral ridge is best developed on the dorsal side, laterally and caudally.

Axis

The centrum is dorsoventrally flattened. A well-developed ridge runs along the ventral surface of the centrum, presumably originating at the base (not preserved) of the dens and continuing sharply to the distal border. This ridge is unlike the slight keel borne by *Lontra*. In *Puijila*, the ridge slightly tapers, becoming level with the ventrally flaring epiphysis. The epiphysis is subovular with a convex rim and a shallowly concave centre. Its ventral border provides irregularity to the shape in the form of a jutting protuberance.

The dens (the odontoid process) is canted dorsally at a thirty-degree angle. The dens is confluent on its dorsal side with a well-developed, but unsharpened, convex ridge extending distally down the centrum. This ridge is interrupted abruptly by a small foramen, before another short ridge finishes off the distal portion. This foramen is also observed in *Lontra*, but the dorsal surface of *Lontra* is flatter, lacking the distinct midline

ridge. The dorsal surface displays paired concavities laterally for the atlantoid transverse ligament.

The cranial articular processes are large, nearly confluent with the dens, and not well-separated from the dens like those of *Lontra*. They face slightly laterally, and are slightly cranio-caudally expanded, unlike the dorsoventrally expanded processes observed in *Lontra*.

Large, paired transverse foramina are present just distally on the lateral surface. Distal to these would be the transverse processes, not preserved in NUFV-405.

Dorsal to the anterior opening of the canal, a dorsocaudally-directed neural arch arises from the cranial articular process. The neural arch of *Puijila* is less craniocaudally wide than that of *Lontra*.

The spinous process is rather complete, but lacks the proximal extension and the distal-most point. Compared to that of *Lontra*, the spinous process of *Puijila* appears less raised and thickened. The caudal articular processes are large, round, only shallowly concave, and ventrolaterally facing. The posterior notch of the vertebral arch appears deep, like those of *Lontra* and *Potamotherium*.

C3-C5

All are preserved, but no neural spines are intact, and the transverse processes are variably fragmentary. The centrum is dorsoventrally flattened. Unlike *Lontra*, C3-C5 of *Puijila* display a sharp midline ridge, again spanning the proximal portion of the ventral surface, before diverging and vanishing around a laterally and ventrally expanded tubercle. This tubercle is confluent with the epiphysis, causing the otherwise ovoid

epiphyseal surface to appear irregular along its ventral margin. The epiphyses are inclined and declined, displaying vertical planes straying from 90 degrees relative to the longitudinal axis of the centrum. The proximal epiphysis is directed slightly ventrally compared to the horizontal plane, while the distal epiphysis is directed slightly dorsally.

The dorsal surface of the centrum is also well-ridged. This ridge is unsharpened and cylindrical. It appears continuous across the longitudinal axis, and, in C3, is not interrupted by a midline foramen. This ridge contributes to the concavity of the laterally adjacent fossae spanning the remainder of the dorsal surface.

The pedicles of C3-C5 are wider than those of *Lontra*. The neural canal is semi-circular. The roof of the neural arch is slightly concave. C3 has a moderately developed median keel, in place of the spine observed in C4-C5. The cranial articular processes are again enlarged, rising well beyond the anterior margin of the centrum. A concavity is present ventro-posterior to this arch on the lateral face of the pedicle. The extension of a large caudal articular process to the transverse process is continuous in C3-C5 of NUFV-405, unlike the condition observed in *Lontra*. The transverse foramina are similar in size and position to those of the axis.

C6

The sixth cervical does not fit into the template of the previous three, and will thus be described individually. C6 loses the ridge on the dorsal surface of the centrum, while the ventral surface displays a reduced keel that does not fade into a defined tubercle. The cranial zygapophyses are directed slightly more medially than C3-C5. A pair of keels run anteroposteriorly along the roof of the neural arch. The transverse

processes are incomplete, but appear plate-like. What remains of the ventral margin is very straight, and nearly parallel with the centrum. A small, but sharp ridge runs between this portion and a gracile, laterally-flaring process level with the ventral surface of centrum.

C7

C7 only preserves the centrum and part of the transverse process. It does not depart in any remarkable way from that of *Lontra* or *Potamotherium*. As typical, C7 lacks the transverse foramen.

Thoracic Vertebrae

The thoracic vertebrae are variably preserved, but all appear to be present in some capacity. Fourteen thoracic vertebrae are present, and this appears to be the presumed complete set in this taxon. The third thoracic is nearly complete. The centra are long and constricted medially, for insertion of the m. longus colli, approaching the spool-shaped condition. The dorsal surface is slightly concave, as re the distal epiphyses. The proximal epiphyseal surface is more circular, also in contrast to the ovoid surface of *Lontra* from this aspect. Demifacets are present just lateral to the anterior and posterior epiphyses, though by T7, they have migrated onto the centrum. The dorsal surfaces of the thoracic centra are remarkably flat. The pedicles are weakly notched and similar in size to *Lontra*, though thicker. The centra are similar in length to *Lontra*, but also dorsoventrally thickened. The neural spines of *Puijila* are more robust than those of *Lontra*, slightly longer, and do not display a sharp posterior extension beyond the level of the caudal

zygapophyses. Like those of pinnipeds, the neural spines of *Puijila* are more caudally directed than those of *Lontra*.

The dorsoventrally expanded transverse processes are more robust than those of *Lontra*, with smaller articulations for the tubercula of the rib. The roots of the transverse processes are thickened, more so than those of *Lontra*, indicating larger laterospinal muscles, as are the pedicles.

Like *Potamotherium*, facets on the transverse processes of the first two thoracic vertebrae are flat, but become increasingly convex on subsequent vertebrae. As one travels posteriorly down the vertebral column, the anterior zygapophyses become more medially situated, migrating away from the transverse processes toward the neural arch. The posterior zygapophyses are laterally broader than those of *Lontra*.

The twelfth, thirteenth, and fourteenth thoracics are well-preserved. They are similar to the lumbar, but lack extensive transverse processes. The 12th is not and displays excavated anterior demifacets lateral to the epiphysis. T11 and T12 have keels instead of neural spines (more like those of the lumbar), and are very spool-shaped, with a rounded ridge running down the ventral surface of the centrum. The last three thoracics lack rib tubercle articulations on their transverse processes. Their posterior zygapophyses are laterally oriented. The anterior zygapophyses become more concave and medially directed with dorsally flaring walls. The anapophyses spines are well-developed. The anapophyses are present, but not fully preserved, while the metapophyses are not strongly developed.

Lumbar Vertebrae

Six lumbar vertebrae are preserved. The centra become increasingly larger travelling posteriorly down the lumbar portion of the vertebral column, and the neural canal becomes smaller. Like the thoracic, the ventral surface of the centrum is laterally constricted, a trait not observed in *Lontra*. The dorsal surface of the centrum is grooved on the midline for basivertebral veins, and indented laterally for the paired anterior internal venous plexus. The pedicles do not reach the level of posterior epiphysis, resulting in large notches, but no articular notch is present. In *Lontra*, the pedicles reach almost the level of the centrum.

Transverse processes are preserved on the second and fifth lumbar vertebra. They are well-developed, being stout dorsoventrally, though slender anteroposteriorly, compared to those of *Lontra*. On the dorsal surface, the middle of the wing rises to a slight keel running transversely. The distal-most extension of the transverse process is pointed anteriorly. The anapophyseal spines (=accessory processes) are not well-preserved, but appear to decrease in size caudally down the spinal column. The metapophyses (=mammillary processes) are also not well-preserved, but appear less longitudinally oriented than those of *Lontra*. Compared to *Lontra*, the zygapophyses of *Puijila* are larger and more mediolaterally elongated. The anterior zygapophyses are more dorsally and less medially directed than those of *Lontra*. The posterior zygapophyses are more ventrally facing with flatter facets. The anterior and posterior borders are u-shaped. Overall the zygapophyses of *Puijila* resemble those observed in *Potamotherium*. In *Lontra*, the notch of the anterior border is laterally broader and less anteriorly-extensive.

This feature is also observed in the posterior zygapophyses, due to the zygapophyses being further apart from each other.

Neural spines are not in tact, but what is left of their bases indicates they were not as anteroposteriorly elongated as those of *Lontra*. A slight ridge is present on the lateral portion of the ventral surface of the centrum, creating a more significantly grooved surface than observed in *Lontra*. The sixth lumbar has no metapophyses and reduced anapophyses.

Sacrum

Composed of three vertebrae, *Puijila*'s sacrum (Figure 1.13) is narrow and wedge-shaped, being superficially similar in size and shape to the sacrum of *Potamotherium*. The sacral canal is very wide and almost slit-like, being significantly less-rounded than the sacral canal of *Lontra*. The anterior-most sacral vertebra is broad, but the sacrum quickly tapers off to a very narrow third sacral vertebra. The first sacral is laterally expanded for iliac articulation, and is only slightly less expanded than that of *Lontra*. The centra of the first two sacral vertebrae are completely ossified. The transverse process of the first sacral is continuous with the lateral expansion of the centrum. The lightly rugose articular surface of the transverse process faces laterally and slightly dorsally. The ventral border of their articular surfaces is straight and slightly flattened, unlike the rounded border of *Lontra*. An anterior, somewhat bulbous semi-circular metapophysis rises above the anterior border of the centrum. This process is also observed in *Potamotherium*. Otherwise, the articular surface is sub-quadrangular, as

opposed to the rounder articular surface of *Lontra*, and extends caudally past the rostral margin of the second sacral vertebra.

On the dorsal surface, the spinous processes are connected by a low sharp ridge. Only the third sacral preserves a complete spinous process, which is much more anteroposteriorly expanded than that of *Lontra*. It is directed slightly posteriorly, though not nearly to the degree of *Potamotherium*. The anterior zygapophysis of the first sacral is larger than that of *Lontra*, flatter, and faces more dorsally and less medially. The other zygapophyses are not well-preserved, but appear to be relatively constricted, flaring less than those of *Lontra*. The posterior most zygapophyses extend beyond the centrum, and house facets facing ventrolaterally, like those of *Lontra*.

Two pairs of ventral sacral foramina lie just cranially above the vertebral intersections, opening dorsally onto the dorsal sacral foramina, which are just lateral to the intermediate sacral crests. The transverse process of the third sacral is less plate-like than that of *Lontra*, present as no more than a thin projection from the centrum extending only slightly beyond the caudal border.

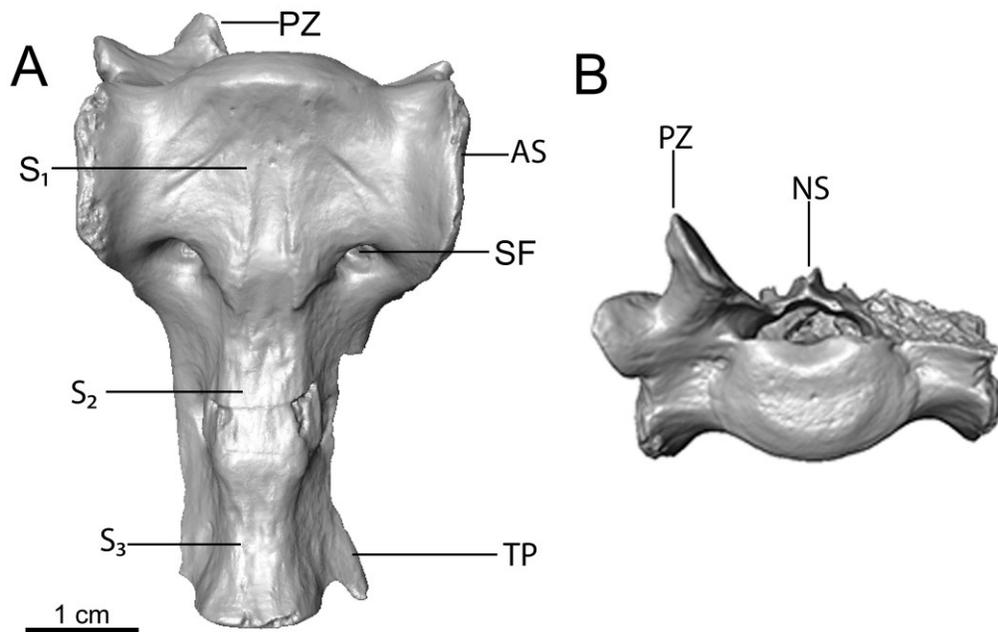


Figure 1.13. Surface scan of sacrum of NUFV-405 in ventral (A) and anterior (B) views.

AS=auricular surface, NS=neural spines, PZ=postzygapophyses, SF=sacral foramina, TP=transverse processes.

Caudal vertebrae

Fourteen caudals are preserved, which appears to represent most of the caudal sequence, although some of the distal most elements appear not to be preserved. The centra of the first four caudals are somewhat dorsoventrally flattened. The body of the first caudal is nearly as wide as it is long. Posteriorly down the column, the caudals lengthen and decrease in width. The first five caudals display discernible transverse processes. The first four continue to display neural arches. The neural arch of the fifth is significantly reduced, producing only a slit like neural canal, and the sixth retains just a miniscule canal (<2mm long). The square plate-like transverse processes are each as wide

as the centrum. They are directed slightly posteriorly, slightly tilted posterodorsally, and possess a latero-posterior extension. The anterior zygapophyses of the first four caudals are relatively large, and directed more medially than vertically, unlike those of *Lontra* and *Potamotherium*. The posterior zygapophyses are preserved only on the first caudal, but are presumably present until the fourth caudal. Unlike those of *Lontra*, the posterior zygapophyses of *Puijila* are not very large, not separated by a notch, and face slightly more laterally. As seen in *Potamotherium*, slight paired ridges run longitudinally down the ventral surface of the centrum. These ridges articulate with the unpreserved or unidentified chevron bones. Neural spines are preserved on the first and third caudals, and would be ostensibly present on the second and fourth caudals. The first displays a short, cranio-caudally elongated spine. The spine of the third is similar to that of *Lontra* in size and shape.

From the fifth caudal onwards, the overall shape changes considerably. The fifth is tall, but not wide, and retains a transverse process. The posterior zygapophyses disappear by the fifth caudal. From the sixth caudal onwards, the transverse processes become slight lateral projections at the base of the centrum. Anterior zygapophyses are present on all caudals, but become reduced and lose their facets, until eventually becoming simple indistinct paired knobs. The chevrons become fused to the anterior-most portion of the ventral surface by the fifth caudal. These chevrons are separated by a shallow groove for the median sacral artery. The centra become more circular in cross-section as one travels down the column. The transverse processes become reduced to lateral extension of the posterior-most portions, disappearing entirely by the thirteenth. Their length remains similar as the centra become slender. Mamillary processes are

present on the anterior portions of the seventh to eleventh caudals, and experience a similar reduction posteriorly along the column. A hemal process is present on all remaining caudals.

Sternum

Eight sternebrae are preserved, with all but the manubrium being nearly completely preserved. The manubrium is missing its cranial half. Unlike those of *Lontra*, the facets for costal cartilage for the first rib of *Puijila* are very expanded laterally, even moreso than *Potamotherium*. Both wings are asymmetrical and set at an angle to the dorsal surface. Ridges run down the midlines of both the dorsal face and the ventral face, the latter of which eventually leads to a presumably pronounced median keel. The caudal articular facet is irregular shaped, unlike the square-shaped facet of *Lontra*.

Sternebrae 2-7 are similar to each other. They are larger and more robust than those of *Lontra* and lack a distinctive ventral keel. Their bodies are nearly round in cross-section and less triangular than those of *Lontra*. The cranial and caudal surfaces are much expanded relative to their bodies, moreso with regards to the caudal surfaces. The caudal surfaces are generally sub-rectangular and dorsoventrally compressed.

The xiphoid process is very robust, and considerably protracted compared to the other sternebrae. The cranial surface resembles an elongated pair of lips. The ventral surface is rounded caudally, and the caudal surface itself is convex.

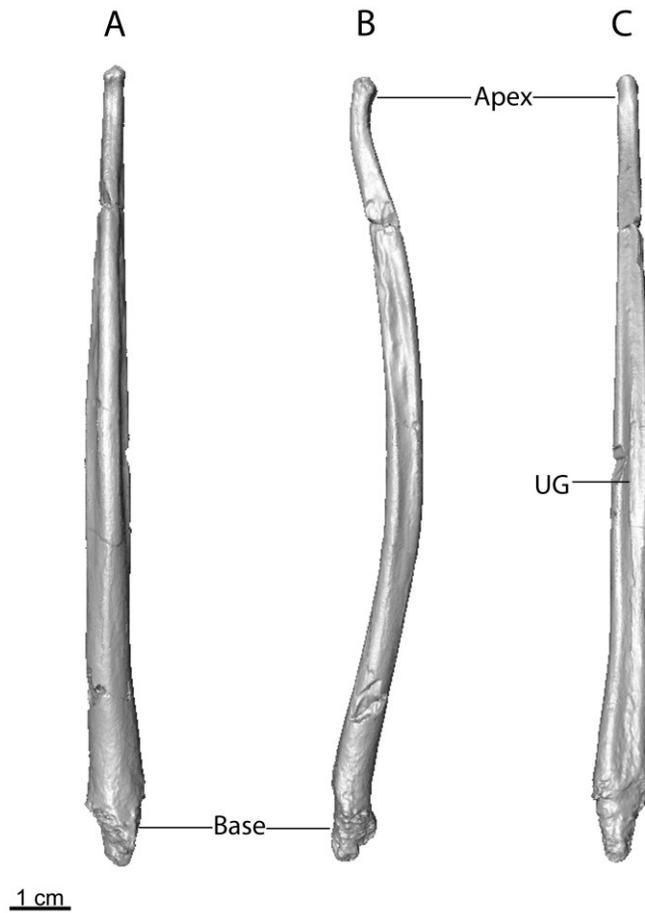


Figure 1.14. Surface scan of baculum of NUFV-405 in dorsal (A), lateral (B) and ventral (C) views. UG=urethral groove.

Baculum

The baculum (Figure 1.14) of *Puijila* is very long and slender, with a sigmoidal shape. The proximal end displays a roughened surface from which a knob projects dorsally. This area is slightly triangular in dorsal and ventral aspects, and broadens as it approaches the beginning of the shaft. From this point onwards, the baculum decreases in width. The ventral surface of the shaft is generally flat, though traversed by a shallow median urethral groove enclosed by slightly raised borders, similar to that of

Potamotherium. The dorsal surface of the shaft is cylindrical with lateral grooves that deepen distally. The shaft dips ventrally as it approaches the distal end. The distal end displays a dorsally directed knob, like that of *Potamotherium*.

Appendicular Skeleton

Scapula

The scapula (Figure 1.15) is incomplete on both sides, but many of its features may be reliably identified. *Puijila*'s scapula is nearly sickle-shaped, approaching the pinniped condition. It is much more dorsocaudally expanded on both sides of the spine than the scapula of *Lontra*. The scapular spine originates at the scapula's proximal border where an elevated section rises and thins out distally, finally terminating just proximal to the distal border as a pair of distinct processes - the metacromion and the acromion. The crest of the spine is somewhat broadened compared to the rest of the spine. The distal end of the spine diverges into a rounded, caudally extending metacromion, and an acromion that is not fully preserved but presumably continues cranioventrally. The two processes are separated from each other by a nearly flat connection, contrasting the ventral notch separating the processes in *Lontra*. A nutrient foramen is present caudally to the spine, just dorsal to the metacromion in lateral aspect, at the junction of the spine and the infraspinatous fossa. The acromion serves as an attachment for the deltoid. The lateral surface of the scapula is further divided by a secondary scapular spine. The secondary spine is unsharpened, appearing similar to that observed in *Potamotherium*.

The infraspinatus fossa is very concave distally, and still considerably concave proximally due to a raised dorsal border and the presence of a secondary spine of Tedford (1976). The infraspinatus fossa is enclosed caudally by a raised caudal border. The caudal border appears as a mediolaterally broadened wall, nearly parallel with the scapular spine, later diverging into the secondary spine and the remainder of the caudal border. Beyond this junction, the caudal border curves strongly laterally, at an angle of about 45 degrees relative from the long axis of the scapular spine. As it reaches the caudal angle, the furthest caudal extension of the scapula, the caudal border is angled about 70 degrees from the scapular spine, producing a small, shallowly concave teres fossa on the lateral surface for teres major muscle insertion. A large infraglenoid tubercle, originating on the cranial portion of the glenoid cavity, runs obliquely along the proximal third of the caudal margin, before converging with the sharp ridge of the caudal border. This tubercle attaches the head of the triceps.

The medial surface (costal surface) is primarily occupied by the subscapular fossa, which appears only shallowly concave between the distally-running muscular lines. Due to the incompleteness of the scapula, a facies serrata is not distinguishable.

The distal end of the scapula is expanded relative to that of *Lontra*. Cranially, a mediolaterally expanded supraglenoid tuberosity rises well above the distal margin, producing a deep basin for the glenoid. This expansion is not observed in *Lontra*. A mediolaterally broadened coracoid process, serving as the attachment of the coracobrachialis, extends significantly medially from the supraglenoid tuberosity, unlike the beak-like coracoid process of *Lontra*. The cranial portion, while expanded compared to that of *Lontra*, remains less expanded than the caudal portion. The caudal portion is

less rounded than that of *Lontra*, but still contributes to the generally ovular glenoid cavity, occupying the entirety of the distal face.

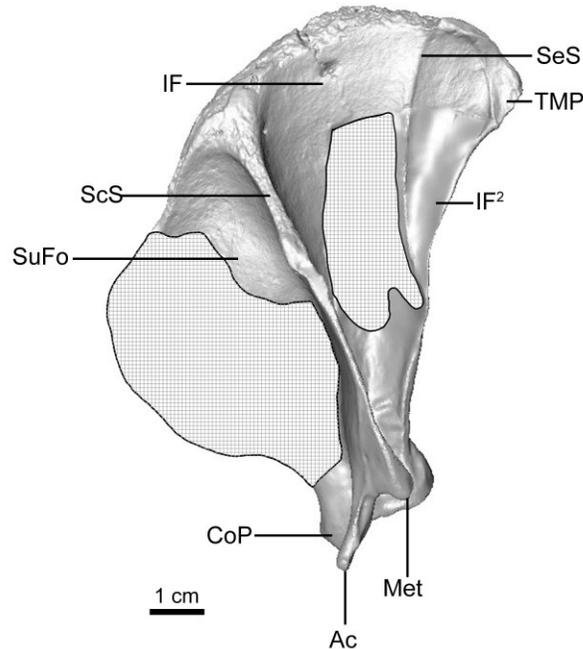


Figure 1.15. Surface scan of right scapula of NUFV-405 in lateral view. Ac=acromion process, CoP=coracoid process, IF=cranial portion of infraspinous fossa, IF²=caudal portion of infraspinous fossa, Met=metacromion process, ScS=scapular spine, SeS=secondary spine of scapula, SuFo=supraspinous fossa. Stippling indicates areas that are not preserved.

Humerus

The humerus (Figure 1.16) is robust, with a maximum length of 9.80 cm, a mediolateral diameter of 0.85 cm, and an anteroposterior diameter of 1.53 cm. The shaft of the humerus is ovular in cross-section and well-curved, though less curved than that of *Potamotherium*. The spherical humeral head of *Puijila* is somewhat constricted

posteriorly, so that the overhanging portion appears less rounded than that of *Potamotherium*, though still significantly more rounded than the ovular overhang observed in *Lontra*. In dorsal view, the lesser tubercle appears nearly confluent with the humeral head. In *Potamotherium* and *Lontra*, the humeral head and lesser tubercle are entirely confluent. In NUFV-405, the two are separated by just a shallow, indistinct groove. The lesser tubercle - the insertion site for the subscapularis muscle - continues slightly down the shaft as a cylindrical ridge, approaching the condition observed in pinnipeds, and most closely resembling the condition observed in *Semantor*. *Enhydra* also displays a short ridge continuing down the shaft, however, the ridge of *Enhydra* is less cylindrical and less robust than those of *Puijila* and *Semantor*. Anteriorly, *Puijila*, like *Potamotherium*, displays a deep intertubercular groove between the humeral head and the inner margin of the greater tubercle, serving as a deep insertion for the supraspinatus. Several small foramina lie deep within this groove. The greater tubercle adjoins the anterolateral border of the humeral head and rises superiorly above it, though it is less raised than that of *Potamotherium*. Posterolaterally to the greater tubercle is a concave square-shaped insertion for the infraspinatus. Laterally, visible scars are present distal to the supraspinatus muscle insertion for insertion of the teres minor. Anteromedially to the supraspinatus insertion is a sagittally elongated, elevated scar for the insertion of the pectoralis muscle.

In anterior view, the pectoral ridge is confluent with the greater tubercle, protruding well anteromedially, not quite to the extent observed in *Potamotherium*, though significantly more so than in *Lontra*. A very sharp deltoid ridge curves gently posterior from the head, and displays scars for the attachment of the deltoids and the

triceps. The two ridges converge, enclosing the broad crest of the greater tubercle, and distally, a deltoid tuberosity more pronounced than that of *Lontra*. The margin of the deltoid tuberosity is sharp along the entire surface, though protruding less posteriorly than that of *Potamotherium*. Distally, the deltoid tuberosity continues sharply to join a large ectepicondyle. On the medial side of the shaft, just distal to the humeral head, lie rugose scars for insertion of the teres major.

The trochlea is anteriorly oriented and rounded on its medial margin, lacking the distinguished ridge displayed by *Lontra*. In ventral view, the trochlea extends well anteriorly beyond the capitulum. On the posterior side, the trochlear trough, between the trochlea and the capitulum, is deep, even more so than that of *Potamotherium*. Extending distally and laterally beyond the trochlea is a large entepicondyle. A large entepicondylar foramen is present on this extension, proximal and lateral to the trochlea. The ectepicondyle of *Puijila* is *Lontra*-like, extending proximally to form the supinator wing, but not laterally beyond the capitulum. On the anterior surface, the medial margin of the supinator wing is keeled, producing a shallow concavity on the wing. This feature is also observed to a lesser degree in *Potamotherium*. Into the lateral surface of the capitulum is excavated a deep round pit, whereas in *Lontra*, only a sliver of a shallow concavity is present, due to the presence of the ectepicondylar process, which *Puijila* lacks.

The olecranon fossa is moderately deep, while the coronoid (radial) fossa is large but shallow. Posteriorly, there is a narrow, deeply excavated area between the trochlea and the entepicondyle. Posteriorly, the capitulum displays a very sharp ridge laterally, like *Potamotherium*.

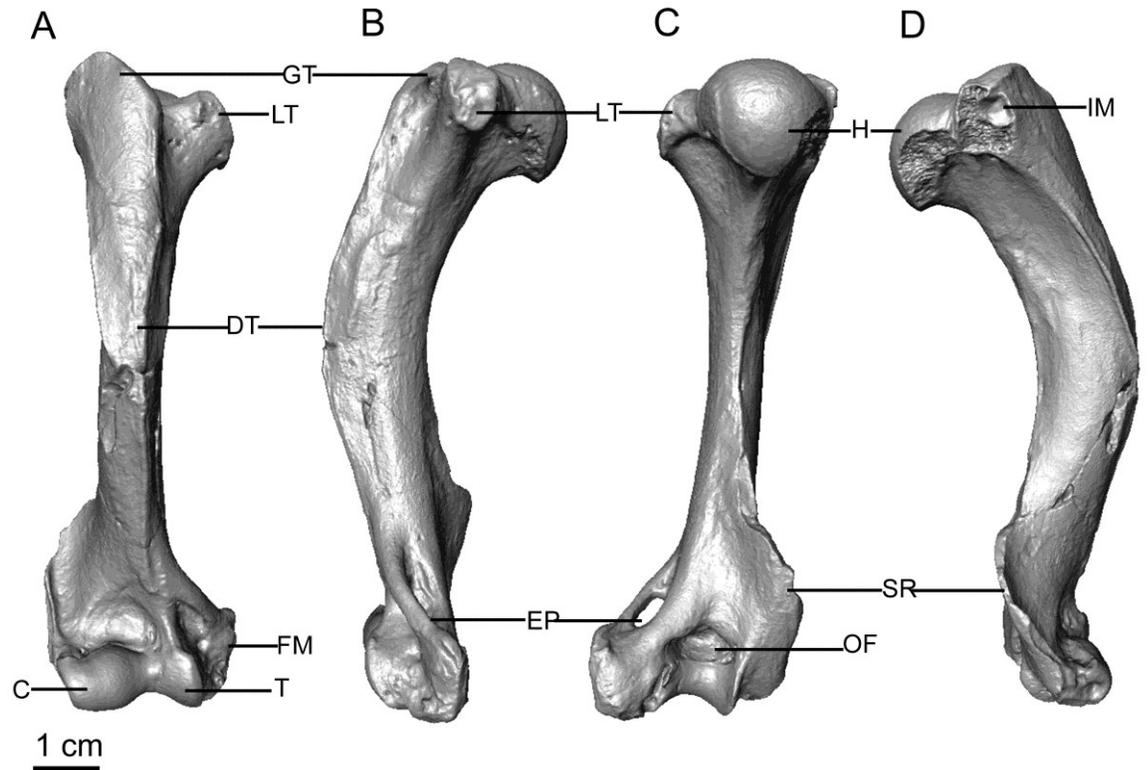


Figure 1.16. Surface scan of right humerus of NUFV-405 in anterior and posterior views.

C=capitulum, DT=deltoid tuberosity, EP=entepicondylar foramen, FM=attachment for flexor muscles, GT=greater tubercle, H=head of humerus, IM=attachment for infraspinatus muscle, LT=lesser tubercle, OF=olecranon fossa, SR=supinator ridge.

Ulna

The ulnar length is 9.732 cm. The ulna (Figure 1.17) is similar in size and general shape to that of *Lontra*. The shaft is sigmoidally curved. The distal half of the shaft is less mediolaterally flattened than that of *Lontra*.

The olecranon is ovular in proximal view, and roughly the same height as that of *Lontra*, but the posterior half is not mediolaterally expanded, contrasting the condition observed in *Lontra*. In lateral aspect, the posterior margin of the olecranon, is not in-line

with the rest of the posterior margin of the ulna, as is the case in *Lontra*, *Potamotherium*, and most terrestrial carnivorans. In *Puijila*, the proximal-most portion of the olecranon extends posteriorly, producing a weak curve along the olecranon's posterior margin. In pinnipeds, the olecranon is flattened and extends strongly posteriorly, producing a strongly curved posterior margin (Berta and Wyss, 1994).

The right ulna displays a large bony growth on the lateral side of the olecranon, that may represent a pathology, though a smaller but similarly-placed projection is also present on the left ulna. Otariids are unique in displaying a proximal ulnar spine on the lateral side of the olecranon. However, the proximal ulnar spine of otariids is no more than a knob restricted to the proximal margin, suggesting it is not homologous with the structure observed in NUFV-405.

The greater sigmoid notch is less deep than that of *Lontra*, and its proximal portion is circular like that of *Potamotherium*, approaching the pinniped condition of a shallow, circular greater sigmoid notch. From posterior view, the radial notch (lesser sigmoid notch) is less flaring mediolaterally than that of *Lontra*. The coronoid process is more narrow than that of *Lontra*, and doesn't flare medially beyond the margin as *Lontra*'s does. Distal to the coronoid is a well-developed scar for the brachialis extending down to the midshaft, similar to the condition observed in *Potamotherium*, though extending less distally than that of crown pinnipeds.

Regarding the proximal half of the shaft, the posterior surface is little more than an unsharpened ridge, approaching the condition observed in *Potamotherium* of a sharp posterior keel. The medial and lateral surfaces are shallowly concave on either side of this ridge.

The lower half of the shaft becomes less flattened and more triangular in cross section. A very wide attachment for the interosseous membrane lies on the lower half. Associated with this expansion is an anterolaterally directed process, absent in *Potamotherium*, and relatively reduced in *Lontra*. Like *Potamotherium*, the anteriorly extending interosseous border is rounder than that of *Lontra*. Anteromedially, a sharp ridge is present on the bottom third of the shaft, reflecting attachment of the pronator quadratus muscle, for which scarring is also present extending anteriorly to the coronoid process.

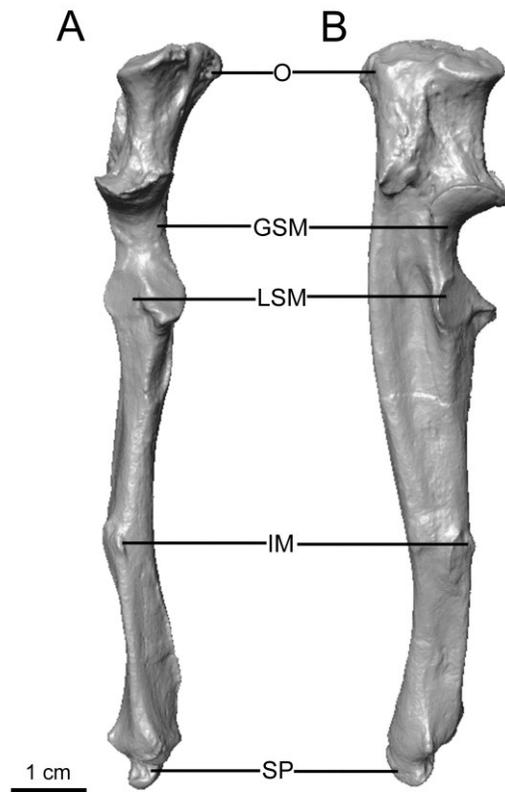


Figure 1.17. Surface scan of right ulna of NUFV-405 in anterior and lateral views. GSM=greater sigmoid notch, IM=interosseous membrane, LSM=lesser sigmoid notch, O=olecranon process, SP=styloid process.

The distal articular circumference is mediolaterally expanded, relative to the condition observed in *Lontra*. The styloid process is rounded at the distal margin, resembling the styloid process of *Potamotherium*, and is anteroposteriorly less narrow than the styloid process of *Lontra*. The styloid process displays facets for the cuneiform (anteriorly) and the pisiform (medially).

Radius

The radius (Figure 1.18) is robust and long, with a maximum length of 7.45 cm and a width at the mid-length of the shaft of 0.84 cm. The proximal head, seen in dorsal view, displays a bean-shaped articular fovea for articulation with the capitulum of the ulna. This articular fovea is concave, with a deep centre and a raised perimeter. On the posterior surface of the fovea is a large proximal ulnar facet. The perimeter of the fovea reaches its highest point above the ulnar facet in *Puijila* and *Potamotherium*, but not in *Lontra*. Just distal to the ulnar facet on the posterior surface exists a well-excavated bicipital pit, separated from the radial head by a short neck. The bicipital pit opens dorsally and somewhat posteriorly. This condition is observed to a similar degree in *Potamotherium*, whereas a significantly shallower bicipital pit is present in *Lontra*. Proximal and adjacent to this pit is a prominent radial tuberosity (the biceps tubercle).

The proximal half of the anterior surface of the shaft is well-scarred for the supinator muscle. The scarring ceases at the pronator teres tubercle, which arises 3/5ths down the shaft. Roughly halfway down the shaft on the lateral face is scarring and a raised dorsoventrally lengthened tubercle for attachment of the interosseous membrane. In *Lontra*, this projection is plate-like and protrudes ~3 mm beyond the shaft. In *Puijila*,

lateral to this feature, a slight/superficial groove runs ventrally, and somewhat anteriorly, likely for the extensor pollicis brevis (Savage, 1957), fading just past the level of the pronator teres process.

In general, the distal portion of the shaft of the radius is robust and curved. The anterior portion of the distal end is very robust and expanded, approaching the condition observed in *Potamotherium*, which itself approaches the pinniped condition. The distal facet is bowled with high edges, resembling the proximal articular facet in its degree of concavity. The antero-medially situated styloid process is large, pointed, and distally-extending. The groove for the extensor indicis is quite deep compared to *Lontra*. A prominent process also exists on the medial surface of the distal portion. This process is present, though reduced in *Lontra*, and absent in *Potamotherium*.

Three grooves are present just dorsal to the distal extremity. On the medial surface is the groove for the tendon of the extensor metacarpi muscle (GEM), which is deeper than that of *Lontra*. On the anterior surface is the groove for the tendons of the extensor communis digitorum and extensor carpi radialis (GE), which is quite concave, slightly moreso than *Potamotherium* and contrasting the flat GE attachment of *Lontra*. Lateral to this groove is a stout knob-like projection. This projection is similarly sized and shaped as that of *Potamotherium*, whereas that of *Lontra* is thin and elongate. On the lateral surface is the groove for the tendon of the extensor indicis muscle (GEI), which is better excavated than that of *Potamotherium*, while *Lontra* displays no concavity. Posterior to this groove, still on the lateral surface, is a well-roughened area representing the distal articular facet. Like *Potamotherium*, and unlike *Lontra*, the facet of *Puijila* does not extend anteriorly onto the shaft.

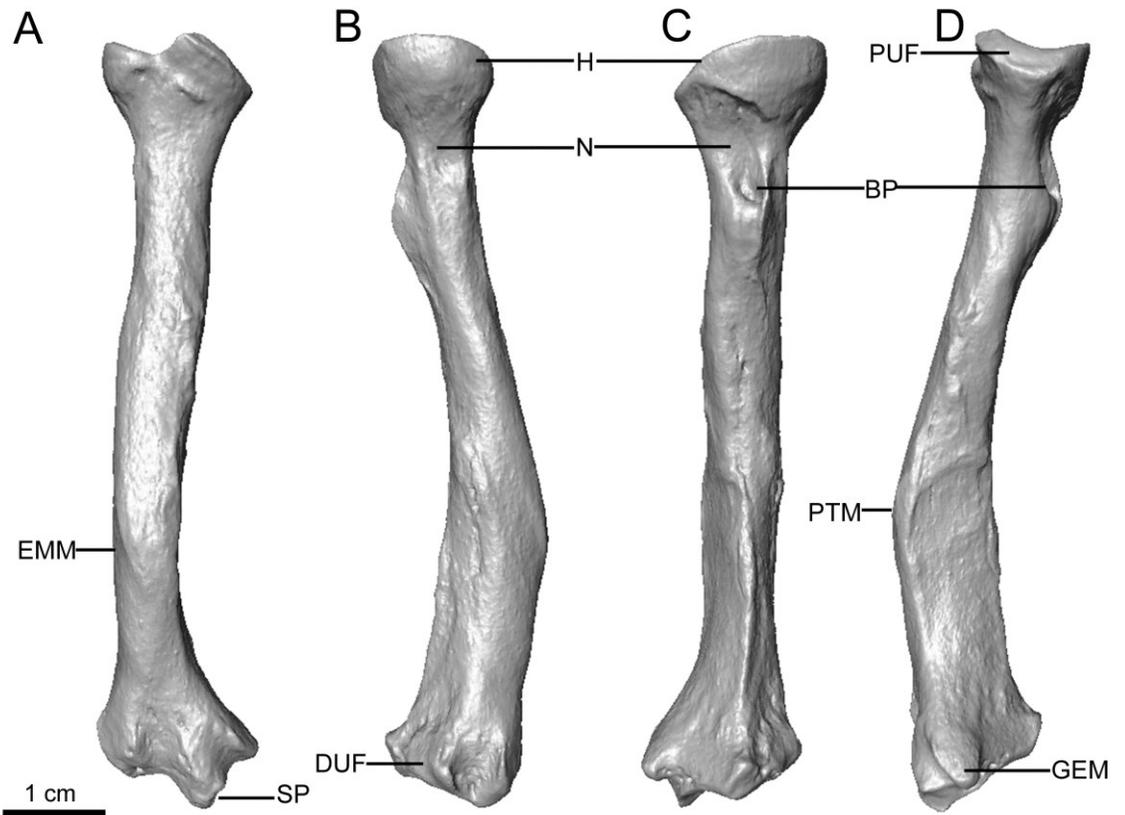


Figure 1.18 Surface scan of right radius of NUFV-405 in anterior, lateral, posterior, and medial views. BP=bicipital pit, DUF=distal ulnar facet, EMM=attachment for extensor metacarpi muscle, GEM=groove for tendon of extensor metacarpi muscle, H=head of radius, N=neck of radius, PTM=attachment for pronator teres muscle, PUF=proximal ulnar facet, SP=styloid process.

Carpals

Present, among the carpals, are the right and left pisiform and scapholunar, the right triquetral, and the right hamate. All are well preserved.

Scapholunar

The scapholunar is more robust compared to that of *Lontra*. Most notably the lateral sesamoid process of *Puijila* is significantly more expanded.

On the ventral surface, the most medial of the facets, the unciform facet is raised compared to the laterally-adjacent magnum facet, and well-separated from it by a ridge. The magnum facet is concave throughout, moreso than that of *Lontra*. Lying just lateral to the magnum facet is a convex trapezoidal facet, contrasting the shallowly concave trapezoidal facet of *Lontra*. The trapezoidal facet of *Puijila* is not continuous with the anterolaterally-located trapezium facet, differing from the confluence of the two facets observed in *Lontra*.

The dorsal surface is divided into a medially-located convex portion, for articulation with the radius, and an anterolaterally located sesamoid process. The convex portion is more bulbous and irregularly shaped compared to most carnivorans. Whereas that of *Lontra* is subrectangular, that of *Puijila* is elongated and vaguely hexagonal with ill-defined edges, displaying processes extending posteriorly and laterally. The convex facet is separated from the sesamoid process by a roughened, irregularly excavated area containing three small foramina (two of which appress the anterior margin of the convex facet). A slight connection between the convex facet and the sesamoid resides at the antero-dorsal junction, but the anterior surface itself divides the two by a prominent groove. Compared to that of *Lontra*, the sesamoid process of *Puijila* is expanded in every dimension, though the mediolateral expansion is greatest.

Pisiform

The pisiform of *Puijila* is much longer than that of *Lontra*. The head, for the tendon of the flexor carpus ulnaris muscle, is very expanded compared to that of *Lontra*, and more rounded in medial and lateral aspect, approaching the condition of *Enaliarctos*

mealsi (Berta and Ray, 1990). The body is rounder and less flattened than that of *Lontra*. Proximally, facets for the triquetrum and ulna are separated from each other by a shallow ridge. The ulnar facet is larger than that of *Lontra*.

Triquetrum

The triquetrum is similar in size and shape to that of *Lontra*. The medial surface displays a small hamatum facet, separated from a larger metacarpal V facet by a sharp ridge. Both facets are shallowly concave. The dorsolateral surface preserves a pisiform facet, larger than that of *Lontra*, and a shallowly concave ulnar facet, which is smaller than the corresponding facet in *Lontra*.

Hamatum

The hamatum of *Puijila* is similar in shape to that of *Lontra*, but smaller. The proximal facet is more sloping than that of *Lontra*. The volar surface is mediolaterally reduced compared to that of *Lontra*, and displays a volar projection, separated from the rest of the element by an encasing groove.

Metacarpals

The metacarpals of *Puijila* are longer than those of *Lontra*. The order of length is: 3>4>2>5>1. Their shafts are all well-rounded in cross-section. The distal ends of metacarpal I-V do not vary considerably, displaying convex facets with a median keel that originates on the volar junction between the facet and the shaft.

MCI

The first metacarpal of *Puijila* resembles that of *Lontra*, with a few notable distinctions. The facet for MCII is visible in proximal aspect, unlike that of *Lontra*. The proximal-most portion of the volar surface is more concave than that of *Lontra*. The proximal articular facet, for the trapezium, slopes palmarly rather than medially, and is slightly more concave than that of *Lontra*.

MCII

The proximal facet is slightly concave, similar to that of *Lontra*. The proximal portion is slightly mediolaterally compressed compared to that of *Lontra*. A prominent bony process is present on the dorsal side, near the proximal facet. This process is less pronounced in *Lontra*.

MCIII

The third metacarpal is less dorsoventrally flattened than that of *Lontra*. The proximal articular facet is mediolaterally compressed compared to *Lontra*. Just distal to the proximal articular facet, on the dorsal surface, a well-pitted area is present.

MCIV

The fourth metacarpal displays a convex proximal articular facet, shaped like that of *Lontra*, though differing from *Lontra* in its high degree of mediolateral compression of the volar half. The shaft is marked by a very distinctive knob on the volar-medial side

near the proximal articular facet. The distal two-thirds of the shaft are at a slight angle from the long axis of the proximal portion, appearing slightly laterally canted.

MCV

The fifth metacarpal of *Puijila* differs from that of *Lontra* in displaying a mediolaterally compressed proximal articular facet that extends further onto the dorsal surface. The shaft is also more extremely laterally canted from the long axis of the proximal articular facet, and less flattened than that of *Lontra*.

Phalanges

Proximal Phalanges

Compared to *Lontra*, the proximal phalanges of *Puijila* are slightly longer but significantly more dorsoventrally flattened. The shafts narrow in the middle before widening toward the distal end. A pair of symmetrical tubercles, one laterally and one medially, extend slightly ventrally and outwards. These tubercles are more pronounced in *Puijila* than in *Lontra*.

Intermediate Phalanges

The intermediate phalanges are very similar to those of *Potamotherium*. The ventral margin is completely flat. The proximal facet rises above the dorsal margin rather than below, and is not curved like that of *Lontra*. An unsharpened ridge on the proximal facet is present on the midline, dividing the facet in two. This ridge begins as a small posteriorly-projecting knob on the ventral margin, and is not observed in *Lontra*. The

proximal portion of the shaft is slightly more mediolaterally broadened than those of *Lontra* and *Potamotherium*. No ventral tubercles are present.

Unguals (Distal Phalanges)

The unguals are very similar to those of *Lontra*, though those of *Puijila* are reduced in size, and unsharpened distally.

Hindlimb

Innominate

Both left and right innominates are largely preserved. The ilium (Figure 1.19) of *Puijila* (length=50.14mm) is shortened compared to that of *Lontra*. The iliac crest (cranial border) flares slightly more laterally than that of *Lontra*. The auricular surface, for attachment with the sacrum, occupies most of the medial surface. It is of a similar size as the auricular surface in *Lontra*, though not as uniformly excavated. On its anterior portion originated the supraspinalis muscle. In lateral view, the iliac wing is only slightly more expanded than the iliac body, whereas *Lontra*'s iliac wing is significantly more expanded than its iliac body. The lateral surface (=gluteal surface) serves as attachment to the gluteal muscles. This surface is completely convex, whereas that of *Lontra* is shallowly concave ventrally, and that of *Potamotherium* is significantly excavated interiorly, due to a thickened ridge running along the dorsal border.

A somewhat excavated pit lies anteriorly adjacent to the acetabulum. This pit is not observed in *Potamotherium* or *Lontra*. Ventral, and somewhat anterior to this pit is a shallower pit flanked anteriorly by a substantial knob-like process (4.31mm x 5.40mm),

protruding laterally to the level of the acetabulum. This process likely denotes the rectus femoris attachment, and is also present in *Potamotherium* (though lateral to the adjacent dorsal to the adjacent pit) and *Ursus* (though without an adjacent pit). On the ventral border, connected to the aforementioned process by a slight ridge, is a prominent iliopsoas tubercle, reflecting the attachment site for the iliopsoas muscle. The ridge connecting the two is not as sharp as that observed in *Lontra* or *Potamotherium*.

The caudal ventral iliac spine is similar to that of *Lontra*. Compared to *Lontra*, the ventral border of the ilium does not display such a degree of confluence with the medial surface. The caudal dorsal iliac spine is less caudally expanded than that of *Lontra*.

The acetabulum is highly cotyloid, in that manner resembling that of *Potamotherium* and *Lontra*. The acetabular notch is, for the most part, laterally facing, but the anterior-most portion is nearly vertical, positioned on the anterior wall of the deep basin, and faces caudoventrally, a condition also observed in *Potamotherium*. The arc of the articular surface for the femoral head is about the same as *Lontra*. Like *Lontra*, the posterior portion of the rim on the ischium is slightly raised.

The posterior portion of the innominate is of a similar length to that of *Lontra*, and longer than that of *Potamotherium*. The bounding of the obturator foramen is incompletely preserved, but the foramen appears sub-ovular like that of *Lontra*.

The ischiatic (ischial) spine differs from that of *Lontra* in displaying a small tubercle on the exterior margin, midway between the acetabulum and the ischial tuberosity. The ischial tuberosity is located further posteriorly than that of *Lontra*, and is reduced and knob-like. The ramus of the pubis is not preserved.

A keel runs along the ischiatic table, gently curved, similar to the curving of the ventro-posterior border. On either side of this keel, the ischium is slightly concave. The ischium appears more massive than that of *Lontra* as it approaches the symphysis. The symphysis pubis is mediolaterally expanded compared to that of *Lontra*. A pubic tubercle and the ramus of the pubis are not preserved.

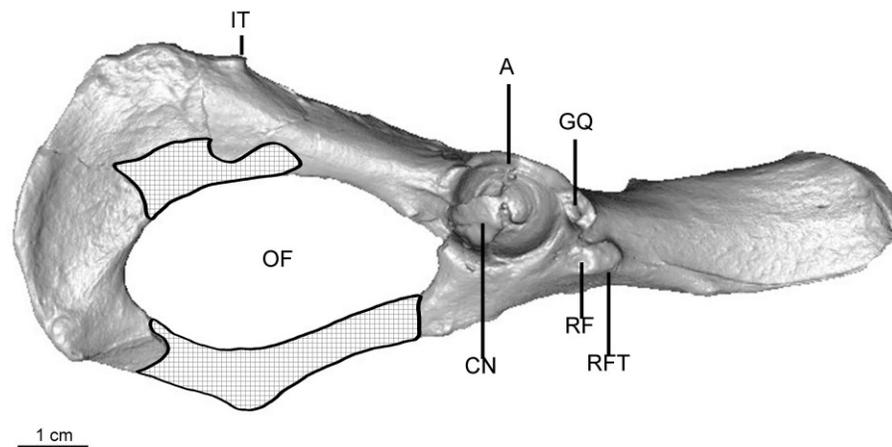


Figure 1.19. Surface scan of ilium of NUFV-405 in medial view. A=Acetabulum, CN=Cotyloid Notch, GQ=gluteus quadratus, Ili=ilium, IT=ischiatric tuberosity, OF=obturator foramen, RF=rectus femoris pit, RFT=rectus femoris tubercle. Stippling indicates areas that are not preserved.

Femur

The femur of NUFV-405 (Figure 1.20) is long, intermediate in length between *Lontra* and *Potamotherium*, but also quite robust. Relative to its estimated body size, the femur is shorter than that of *Lontra*. *Puijila*'s femoral shaft is rounder and less anteroposteriorly compressed than that of *Lontra*. This compression is more significant on the anterior surface of *Puijila*'s femoral shaft, while the posterior surface is more expanded.

The femoral head of *Puijila* is spherical and directed medially and somewhat cranially, like that of *Lontra*, and retains a small, postero-medially facing fovea for the

ligamentum teres femores. This pit is deep, round, and anteroposteriorly expanded, resembling that of *Potamotherium*, and unlike the larger, cranio-caudally expanded fovea of *Lontra*. In anterior aspect, the lateral margin of the femoral head is obliquely angled compared to the shaft, and somewhat curved. This resembles the condition observed in *Lontra*, whilst the margin of *Potamotherium* is nearly parallel to the shaft. Uniting the head with the diaphysis is an obliquely oriented neck, slightly smaller in proximo-distal width than the head, and longer than the compressed neck of *Potamotherium*. Lateral to the head, and reaching up to the same level, is the greater trochanter, separated from the head by a notch that is similar to that of *Lontra*, but more rounded. On the lateral surface, muscle scarring is present from the greater trochanter down to the level of the lesser trochanter, for insertion of the piriformis and gluteal muscles. A deep, medially-expanded trochanteric fossa is present at the posterior surface, just medial to the greater trochanter. The trochanteric fossa is much broader than that of *Lontra*, but less broad than that of *Potamotherium*. Unlike *Lontra*, the trochanteric fossa is nearly entirely confluent with the neck, with only a small rugosity separating the two at the proximal margin. In *Potamotherium*, a larger raised bump is present in this area, though it is not nearly as extensive as the ridge observed in *Lontra*, which runs obliquely to the level of the second trochanter. Along the border separating the fossa from the greater trochanter were inserted the gemelli and obturator muscles, responsible for abduction and rotation of the femur/lower limb. The lesser trochanter, serving as the insertion for the iliopsoas muscle, is situated 8.55 mm distal to the head. The lesser trochanter is extremely medially protruding, displaying a rounded eminence not observed in any of the compared specimens. The lesser trochanter of *Potamotherium* is somewhat protruding, but not

nearly to the degree observed in *Puijila*. Immediately anterior to the lesser trochanter is a shallow fossa for the vastus medialis attachment. In *Potamotherium* this fossa is broader and more concave. Distal to the lesser trochanter is an impression for the insertion of the quadratus femoris. On the lateral surface, level with the lesser trochanter, is a slight expansion, interpreted as a vestigial third trochanter, a likely insertion for the gluteus superficialis muscle. From here, a ridge on the anterolateral border connects with the central tubercle of the greater trochanter.

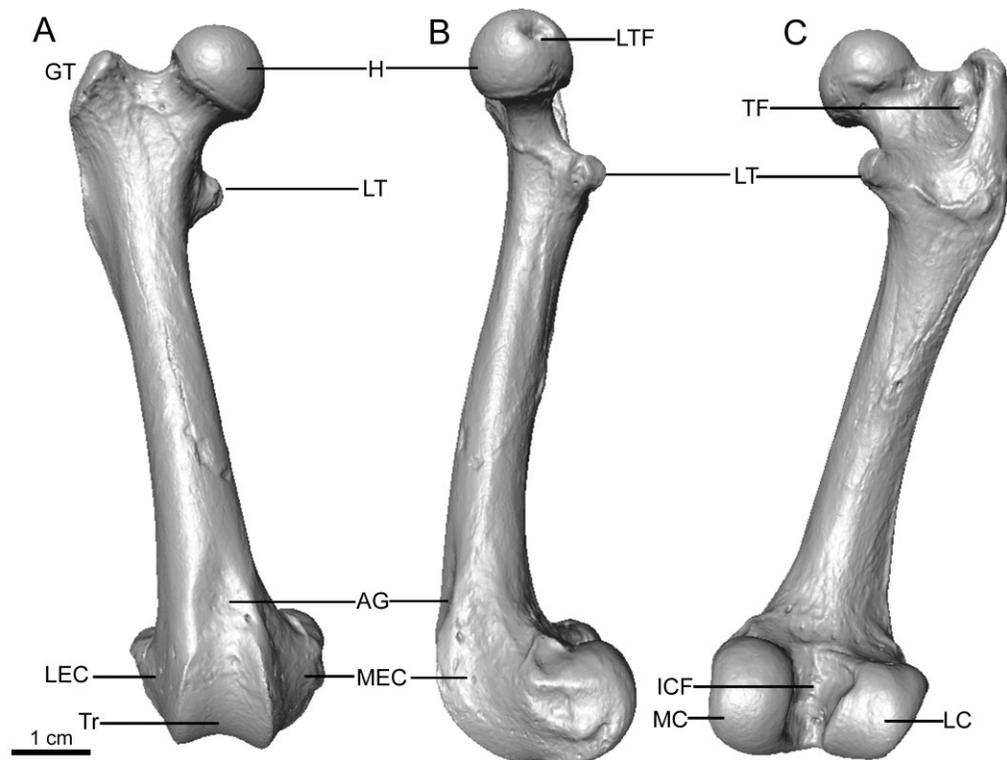


Figure 1.20. Surface scans of right femur of NUFV-405 in anterior, lateral, and posterior views. AG=fossa for the articularis genus, ICF=intracondylar fossa, GT=greater trochanter, H=femoral head, LC=lateral condyle, LEC=lateral epicondyle, LT=lesser trochanter, MC=medial condyle, MEC=medial epicondyle, TF=trochanteric fossa, Tr=trochlea of femur.

The shaft's posterior surface is heavily roughened, representing a reduced *facies aspera*. The *facies aspera* is enclosed by a lateral lip and a medial lip. The lateral lip

begins at the greater trochanter, travelling down the posterolateral border before becoming obscured as it approaches the lateral condyle. The less prominent medial lip begins about 1cm below the lesser trochanter, becoming obscured about two thirds of the way down the shaft.

Distally, the posterior surface displays a relatively flat popliteal surface on the distal half of the shaft, though it is not as flat as that of *Lontra*. The distal condylar region is very broad. The medial condyle extends further medially than the lateral condyle extends laterally, and also extends further distally and posteriorly than the lateral condyle.

The trochlea for the patella is quite concave, more so than *Lontra* and *Potamotherium*. The ridges of the trochlea are sharp, running antero-proximally to the border of the diaphysis. A fossa, confluent with the trochlea, continues proximally up the shaft, for insertion of the articularis genus muscle, which is involved with leg extension. This fossa is also observed in *Potamotherium*, although *Potamotherium*'s is deeper.

Into the broad medial epicondyle would be inserted the head of the gastrocnemius. The proximal surface of the lateral epicondyle is flatter than that of the medial epicondyle, and from it arose the lateral head of the gastrocnemius. On the posterior surface, between the condyles, is a very deep intercondyloid fossa, representing the attachment of the cruciate ligaments. This fossa is narrower than that of *Lontra* or *Potamotherium*. From posterior view, the condyles are similarly-shaped and oriented in the same direction, like the condition observed in *Lontra*. Like *Potamotherium*, *Puijila* lacks a lateral supracondylar tuberosity.

Patella

The patella is very similar in shape to that of *Potamotherium*. Neither taxon displays a patella as elongated or triangular as that of *Lontra*. *Puijila* displays a small notch on the distal lateral margin. A well-developed groove runs dorsoventrally down the anterior face, while the posterior face is very smooth and shallowly concave. The patella of *Puijila* is anteroposteriorly thicker on its proximal half.

Tibia

The tibia (Figure 1.21) is longer than that of *Lontra*, but also more robust. *Puijila*'s tibia is expanded at both ends. The proximal portion of the shaft is gently curved and triangular in cross-section. The head is of a similar breadth as that of *Lontra*. The condyles extend a similar distance posteriorly compared to each other, unlike the condition observed in *Lontra*, in which the lateral condyle does not extend far beyond the posterior margin of the tibia. The articular facets upon both condyles in *Puijila* are semi-circular in shape. The lateral facet is convex, while the medial facet is shallowly excavated. On the articular surface, a narrow spine arises from the posteromedial border of the lateral condyle, running anteriorly along the proximal surface. At about its midlength it is intercepted by a sharp intercondylar eminence. Though sharp, the intercondylar eminence barely extends above the level of the condyles. Anterior to the intercondyloid eminence is the area intercondylus cranialis, and posterior is the area intercondylar caudalis. Both foveas are shallow and similar to those of *Lontra*, though the posterior of *Puijila* is less ventrally sloping toward the margin. This represents an intermediate between *Lontra*, and *Potamotherium*, the latter of which displays a horizontal posterior fossa without ventral sloping.

The ventral surface of the lateral condyle displays a concave fibular facet. Posteriorly, distal to the articular surface, the concave popliteal notch is sandwiched by the posterior ends of the condyles. In association with the enlarged lateral condyle, the popliteal surface of *Puijila* is particularly concave, to a greater degree than observed in *Potamotherium* or *Lontra*.

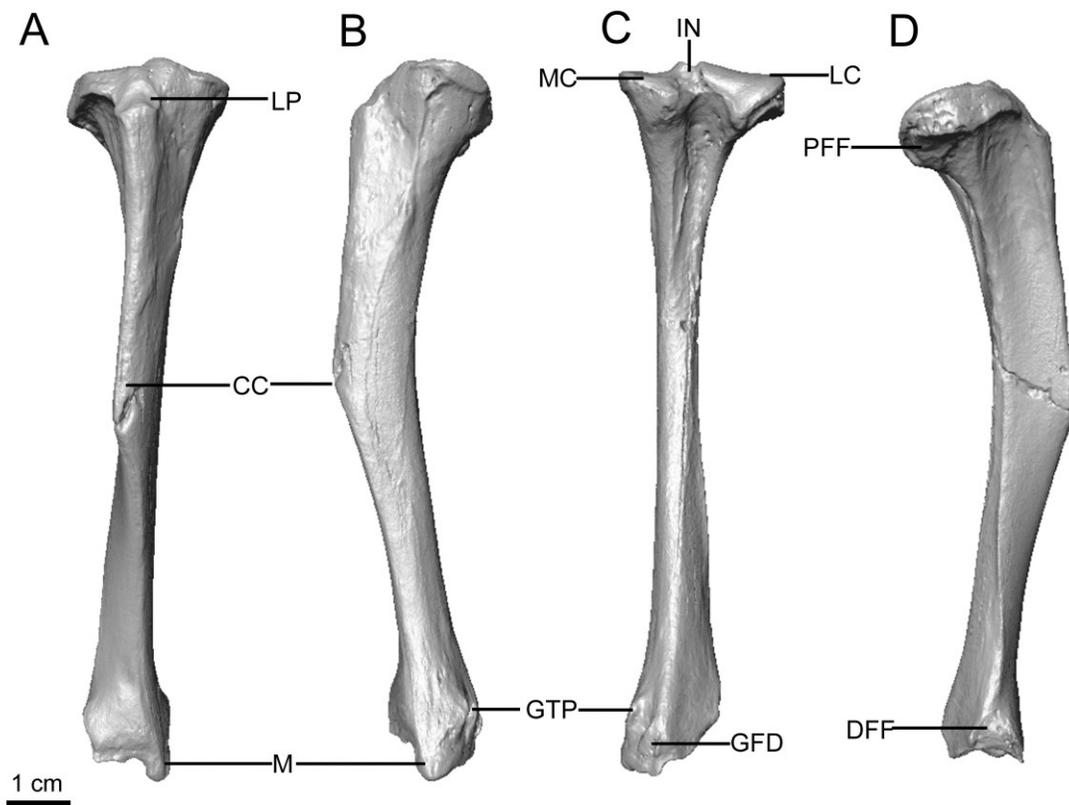


Figure 1.21. Surface scans of right tibia of NUFV-405 in anterior, medial, posterior and lateral views. CC=cnemial crest, DFF=distal fibular facet, GFD=groove for the tendon of the flexor digitorum longus, GTP=groove for the tendon of the tibialis posticus muscle, IN=intercondylar notch, LC=lateral condyle of Tibia, LP=ligamentum patellae, M=medial malleolus, MC=medial condyle of tibia.

Anterior to the condyles arises a prominent tibial tuberosity, more prominent than that of *Potamotherium*, and more ventrally located than that of either *Potamotherium* or

Lontra. The tibial tuberosity extends to the cnemial crest, which projects strongly from the proximal half of the shaft's anterior surface, serving as an attachment for the biceps femoris. The cnemial crest appears very sharp, exaggerated by a deeply excavated lateral surface. This remarkably concave lateral surface is also observed in *Potamotherium*, and likely serves as an origin of the anterior tibialis and extensor digitorum. The posterolateral border is marked by a ridge from which the flexor digitorum longus originated. Heavy scarring is visible on the posteromedial border.

In posterior view, the distal half of the shaft is rounded, and less scarred than the proximal half. The distal epiphysis is wider than the shaft, but, like *Potamotherium*, not to the extent observed in *Lontra*. Like in *Potamotherium*, two grooves traverse the medial border of the distal extremity, the more anterior of which is larger and likely serves as an attachment for the tibialis posterior. The more posterior of the two likely serves as an attachment site for the flexor digitorum longus. Most carnivores display only a single groove doubling as the attachment site for both muscles. The ridges encasing the grooves do not extend as posteromedially as those observed in *Lontra*.

The lateral border of the distal extremity displays a small fibular facet. Unlike *Lontra*, the fibular facet of *Puijila* is laterally facing, and does not extend laterally beyond the margin of the tibia. In medial view, the medial malleolus displays a small notch on its distal most extension. This small notch is observed in *Potamotherium*, differing from the continuous, sloping margin of *Lontra*'s medial malleolus. In ventral view, the distal surface, for articulation with the astragalus, is deep, displaying a very slight keel separating the medial and lateral basins. The distal surface is similar in shape to that of *Potamotherium*, with similar borders, most notably a straight posterior margin, as

opposed to the triangular posterior margin of *Lontra*. *Lontra*'s distal articular surface is more laterally expanded than those of *Puijila* and *Potamotherium*.

Fibula

The fibula is long and slender. The shaft of the fibula is nearly straight, unlike the more bowed fibula of *Lontra*. In *Puijila*, the midshaft is slightly thicker and rounder than the shaft of *Lontra*, approaching the more robust fibulae of *Enaliarctos* and *Semantor*. The proximal portion of *Puijila*'s shaft forms a thin triangle in cross section, with the apex pointing posterolaterally.

The articular facet for the tibia is long and generally concave, though shallowly grooved proximally. It is expanded anteriorly, bearing a process for the peroneus longus muscle. A small tubercle projects posteromedially, just ventral to the articular facet. This tubercle is even smaller than that of *Lontra*. A large oval tubercle lies on the posterior ridge. It is 8 mm in dorsoventral length. *Puijila*'s fibula lacks the lower medial trochanter occurring in *Lontra* about a quarter of the way ventrally down the shaft. The distal two thirds of *Puijila*'s shaft are rounded with a sharp anterior ridge.

The lateral malleolus is similar in expansion to *Lontra*. The medial-posterior border of the lateral malleolus is semi-circular. A process extends laterally from the shaft – the processus lateralis fibulae – also observed in *Potamotherium*, *Enaliarctos*, phocids, and ursids. Disto-posterior to this process is excavated a deep longitudinal groove, for the tendons of the peroneus brevis and longus, as well as the extensor digitorum lateralis.

The distal tibial facet is small and medially directed. Just posterior to this facet is excavated a ventromedially directed articular facet for articulation with the astragalus.

These are confluent in *Lontra*.

Tarsals

Astragalus

Compared to *Lontra*, the astragalus of *Puijila* (Figure 1.22) is similar in size and shape. Distally, it displays an ellipsoidal, mediolaterally elongated head borne on a dorsoventrally compressed neck, arising from the body at an oblique angle. The head bears a convex navicular facet, similar in size and shape to that of *Lontra*.

The astragalar body is rectangular in dorsal aspect, and less broad than that of *Lontra*. The trochlear groove, running along the dorsal surface, is not as centrally notched as that of *Lontra*. The lateral malleolar surface is less rounded than that of *Lontra* and reduced dorsoventrally. This surface bears a smoothed, slightly concave fibular facet on its distal half. The fibular facet protrudes laterally from the lateral surface, the rest of which is also concave for ligament attachment.

The medial malleolar surface bears an arcuate facet for the medial malleolus. This facet does not display a ventro-distal extension observed in *Lontra*. Proximally, the arcuate facet is confluent with the trochlea. In dorsal view, the proximo-ventral portion of the arcuate facet flares proximally, a condition observed in *Potamotherium*, but not in *Lontra*.

Small astragalar foramina are visible on the distal and volar surfaces. The foramen on the plantar surface is situated within a deeply excavated recess surrounded by facets. These foramina are also present in *Potamotherium*, but absent in *Lontra*. Running along the lateral half of the volar surface is the astragular facet, which is smooth and deeply bowled. Shared between the body and the neck, on the volar surface, is present a slightly concave, quadrangular articular facet, separated from the navicular facet of the head by a distinctively pitted area. This facet articulates with the calcaneum. The trochlea is also visible in volar view, encroaching past the proximal margin as a grooved surface for the tendon of the flexor digitorum longus (Savage, 1957).

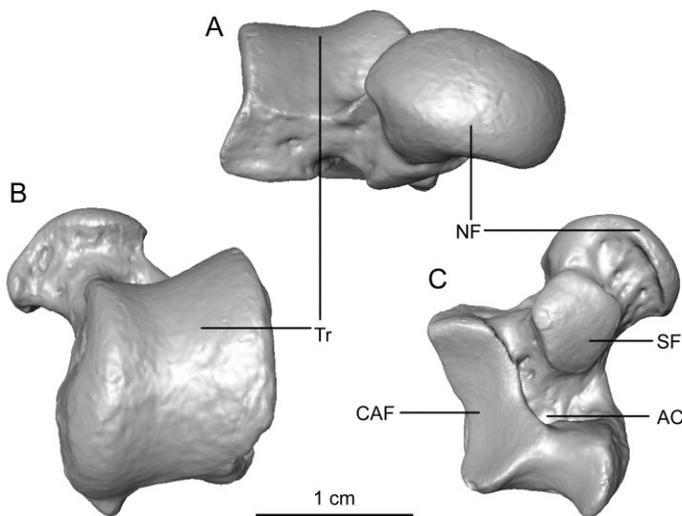


Figure 1.22. Surface scans of right astragalus of NUFV-405 in dorsal, anterior and ventral views. AC=astragalar canal, CAF=calcaneoastragalar facet, NF=navicular facet, SF=sustentacular facet, Tr=trochlea of astragalus.

Calcaneus

Like *Lontra*, the proximal head of *Puijila*'s calcaneus (Figure 1.23) is subquadrangular and not significantly mediolaterally expanded compared to its body.

This contrasts with the condition observed in *Potamotherium*, which exhibits a sub-triangular head in proximal aspect. *Lontra* displays a distinctive bowled groove between the medial and lateral processes of the head. This groove is absent in *Potamotherium* and *Puijila*, causing their medial and lateral processes to become indiscernible across their flattened heads.

The proximal half of the tuber is less mediolaterally flattened than that of *Lontra*. More distally, *Puijila* displays two facets on the dorsal surface for articulation with the astragalus. These facets are smaller than those of *Lontra*. Running between these facets is a deep groove for the interosseous ligament.

The lateral articular facet is convex and similar to those of *Lontra* and *Potamotherium*. It appears to share the lateral margin with the peroneal tubercle, which is not preserved on either the right or the left calcaneus. Anteromedially, a broad, distinguished groove, for the interosseous ligament, separates this facet from a more medially situated sustentacular facet. The sustentacular facet is smaller and less bowled than that of *Lontra*, and is situated on a medial projection of the calcaneus - the sustentacular process. Both facets articulate with corresponding facets on the astragalus. Medially to the medial astragular facet is a groove for the flexor digitorum longus (Savage, 1957). Lateral to this groove, on the medial portion of the ventral surface, is a slightly concave facet, possibly for articulation with a navicular ligament (Savage, 1957). A shallowly concave cuboid facet is present upon the distal surface. The cuboid facet is mediolaterally compressed compared to those of *Lontra* and *Potamotherium*, and appears taller than it is wide.

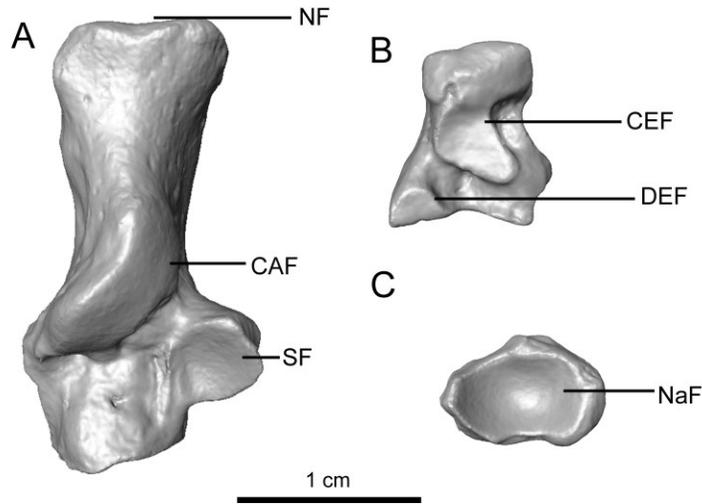


Figure 1.23. Surface scans of calcaneus, cuboid, navicular. CAF=calcaneoastragalar facet, CEF=central ectocuneiform facet, DEF=distal ectocuneiform facet, NF=navicular facet, SF=sustentacular facet.

Navicular

The navicular (Figure 1.23) is similar to that of *Lontra* and *Potamotherium* in size and shape, being generally ovular in appearance. The dorsal surface is very concave, serving as an articulation for the convex navicular facet of the astragalus. The rim of the navicular surface reaches its apex laterally, where it comes to a pointed tip. This extension the dorso-anterior corner of a well-developed facet for articulation with the cuboid, present on the lateral half of the posterior surface. The pointed tip is absent in *Potamotherium* and *Lontra*. The cuboid facet displays a posterior extension, making the facet relatively elongated compared to that of *Lontra*, *Enhydra*, or *Odobenus*. The rim also rises, as it does in *Lontra* and *Potamotherium*, with an eminence on the medial surface for the interosseous ligament.

The distal surface bears a large, generally convex faceted area, extending from the anterior half of the medial margin to the entirety of the lateral margin. The laterally located facet articulates with the ectocuneiform. The small unfaceted posteromedial quadrant is well grooved for the interosseous ligaments. The medial facet articulates with the entocuneiform. Positioned in between the other facets, and separated from them by slight keels, is a facet for articulation with the entocuneiform. Unlike *Lontra*, the navicular of *Puijila* lacks a defined posterior process. In *Puijila* this facet is confluent with the posteromedial facet, and extends further posterodistally.

Cuboid

The cuboid of *Puijila* (Figure 1.23) is very similar to that of *Potamotherium*. It is subquadrate and slopes medio-distally. The proximal surface is covered by a convex facet for articulation with the calcaneum. This facet is semi-circular, and continues distally as a lobe onto the lateral portion of the posterior surface. The medial surface is occupied by two well-defined facets and a third less well-defined facet. The facet on the proximal third of the surface is slightly convex, and articulates with the navicular. A slight crest runs anteroposteriorly across the facet. Adjoining this distally is a somewhat concave, obliquely-oriented facet for articulation with the navicular (or ectocuneiform; see Savage, 1957). Antero-distally to this facet is a small, flat facet also for articulation with the ectocuneiform. This resembles the condition of *Potamotherium* and pinnipeds, but musteloids lack the definition of this distal facet.

The lateral surface bears a wide, deep groove (the sulcus tendinus) for the tendon of the peroneus longus muscle. Proximal to the sulcus is a salient ventral tuberosity

(plantar process) overhanging the sulcus, stretching from a cylindrical ridge present on the ventral surface. Between the cylindrical ridge and the proximal articular facet, within an excavated region, lies a small, flat, ill-defined circular facet.

The distal surface comprises an arch-shaped, concave facet, with a small notch on the medial margin, for articulation with the 4th and 5th metatarsals. This facet is about as long as it is wide, and is not traversed by the ridge observed in otariids, odobenids, and *Potamotherium*.

Ectocuneiform

The ectocuneiform is very similar to that of *Potamotherium*. The proximal facet is concave for articulation with the navicular. The distal facet is shallowly concave for articulation with the 3rd metatarsal. Ventrally to this distal facet, is a ventrally-extending process, continuing onto the ventral surface, where it is bordered posteriorly by a moderately-developed groove for the peroneus longus tendon. The lateral side displays a pair of small, indistinct facets for articulation with the navicular. The medial side displays a facet for articulation with the mesocuneiform, and a pair of small facets on the ventral margin for the second metatarsal.

Mesocuneiform

The mesocuneiform is the smallest of the tarsal bones by a considerable margin. It is rhomboidally shaped. The faceted proximal and distal ends are of similar lengths and shallowly concave. The proximal end is narrow, but quickly broadens, as a sharpened triangular extension protrudes well beyond the rest of the medial margin. The ventral half

of the surface is mediolaterally constricted. The distal end is pea-shaped, narrowing ventrally. The proximal and distal surfaces converge upon a shared ventral margin. The medial surface bears a saddle-like articular facet on the dorsal half of its surface for articulation with the ectocuneiform. The lateral surface is lightly faceted for articulation with the entocuneiform.

Entocuneiform

Only the right entocuneiform of *Puijila* is preserved. The entocuneiform is a transversely compressed bone, vaguely rhomboidal, similar to that of *Potamotherium*. The proximal articular surface is concave for articulation with the navicular. The distal articular facet is also bowled dorsoventrally, but not concave mediolaterally, and articulates with the first metatarsal. The ventral margin is nearly straight, while the dorsal margin reaches an apex towards the distal end, tapering off slightly distally and significantly proximally. The proximal dorsal corner of the lateral face bears a small, convex oblong-shaped facet for articulation with the mesocuneiform. This facet faces laterally and dorsally. Its dorsal portion is confluent with the proximal articular facet. The ventral half of the lateral surface is concave

Metatarsals

The metatarsals of *Puijila* are longer than those of *Lontra*. The order of length is 4>3>2>5>1.

MTI

The first metatarsal of *Puijila* is appreciably longer than that of *Lontra*. *Puijila*'s first metatarsal displays a well-developed proximal end with mediolateral expansion. This modification is not observed to this extent in *Lontra*. Laterally on this end is a convex facet for articulation with the second metatarsal. This facet curves dorsally and laterally, extending slightly onto the dorsal surface. The rest of the proximal surface is covered by a shallowly concave facet for articulation with the entocuneiform. The ventral surface of the proximal end bears a wide groove lying between the ventral projections of these two facets, causing a notch to appear across the ventral margin in proximal aspect. The shaft is nearly round in cross-section, eventually leading to the distal articular surface which is typical of a terrestrial Carnivoran in displaying a slight central keel.

MTII

The second metatarsal is only slightly longer than that of *Lontra*. The proximal end is mediolaterally flattened. The proximal articular surface displays a well-defined, though shallow, groove for mesocuneiform articulation. This groove faces posteromedially and is not visible in lateral view. The nearly flat lateral surface is separated from the proximal surface by a sharp keel. The lateral side bears two facets, one ventrally located and one more dorsally located, for articulation with the ectocuneiform, and shallow grooves for articulation with the third metatarsal. A shallowly excavated facet is present on the medial side for articulation with the first metatarsal. The proximal portion of the dorsal surface displays a small dorsally-projecting eminence.

MTIII

The third metatarsal is also only slightly longer than that of *Lontra*. Its proximal surface is dorsoventrally elongated, presenting a facet for the ectocuneiform. The lateral margin is significantly notched. Without this notch, the proximal end would appear roughly trapezoidal. The proximal surface is canted slightly towards the medial margin. On the lateral surface, just anterior to the proximal margin runs a well-defined groove separating a pair of facets. The ventrally positioned facet is shallowly concave, and faces dorsolaterally. The larger, remarkably concave dorsal facet is excavated dorsally into the dorsal wall and medially into the lateral wall. It is directed laterally and somewhat ventrally. This facet is larger than that of *Lontra*. Together, these two facets serve for articulation with the fourth metatarsal. The medial surface is also notched, but only slightly, and is still relatively straight. The medial side displays a slight pit and an unremarkable facet for articulation with the second metatarsal.

MTIV

The proximal surface of the fourth metatarsal is convex, obliquely oriented, dorsoventrally elongated, and rhomboidal for articulation with the cuboid. The proximal surface slopes slightly dorsally, so that it is concealed in ventral aspect. Anteromedially, on the dorsal surface, a bulbous projection arises, confluent with the shaft, and directed slightly posteriorly. The lateral side of the proximal end is well-excavated for articulation with the fifth metatarsal. A shallowly concave facet lies on the ventral surface. Between that facet and the aforementioned projection is a broad trench.

MTV

Among the metatarsals of *Puijila*, it is the fifth that most closely resembles the corresponding metatarsal of *Lontra*. Its proximal surface slopes in dorsally and is irregularly shaped, with a convex triangular facet for the cuboid, differing from *Lontra* only in the placement of a shallowly concave pit located laterally to the facet. Rising above this facet is an indistinct knob-like process, and distal to that is a larger knob-like process on the medial margin. Distally and laterally to this large process is another small projection on the dorsal surface of the metatarsal. The fifth metatarsal of *Puijila* extends slightly more ventrally than that of *Lontra*.

Hind Proximal Phalanges

In descending order, the length of the hind proximal phalanges is as follows: 4>3>2>1>5. *Puijila* does not display the size disparity between hind proximal phalanges observed in *Lontra*. The hind proximal phalanges are longer and more dorsoventrally flattened than those of *Lontra*. They are D-shaped in cross-section, displaying a concave articular surface. The undersides are flat, and slightly more rounded dorsally than those of *Lontra*. The lateral and medial borders are not straight. Well-developed processes extend medially from the distal half of the volar surface. The distal portion of the shaft widens mediolaterally.

Hind Intermediate Phalanges

The intermediate phalanges of *Puijila*'s hind limb are similar to those of *Lontra*, but more robust. The body is of a similar thickness to that of *Lontra*, but is slightly

mediolaterally expanded and not as flat as that of *Lontra*, though more dorsoventrally flattened than that of *Potamotherium*.

Hind Ungual Phalanges (Distal Phalanges)

The unguals of the hind limb are similar to those of *Lontra* and *Potamotherium*, displaying a large foramen, an unsharpened tip, and an ungual process that is not significantly curved. Assignment of unguals is difficult. Only three are preserved, and have been tentatively identified as the first and fifth unguals of the right hindpaw, and the fifth ungual of the left hindpaw.

Discussion of Skeletal Morphology

Osteologically, *Puijila darwini* most closely resembles *Potamotherium*. Despite superficially appearing less aquatically-adapted than *Potamotherium*, *Puijila* shares a handful of traits with *Enaliarctos*, not found in *Potamotherium*. These include the presence of an alisphenoid canal, presence of an interbullar septum, a narrow tympanic crest that protrudes well into the tympanic cavity, an inflated auditory bulla, lack of a lower first incisor, a cylindrical lesser tuberosity of the humerus, and a more extreme femoral condylar angle. Of course, *Potamotherium* shares a suite of characters with *Enaliarctos* to the exclusion of *Puijila*, but many of these appear to manifest a strong biomechanical signal (v-shaped deltopectoral ridge, short and flattened femur).

Comparisons between *Puijila* and *Semantor* suggests a wide evolutionary distance between the two. Like the other pinnipedimorphs, *Semantor macrurus* displays a transitional morphology, but further approaches crown pinnipeds in its possession of a

shorter, flatter femur displaying a pinniped-like reduction of three biomechanically-significant features: the second trochanter, the fossa for the ligamentum femoris and the trochanteric fossa (Berta, 1991). The tibia and fibula of *Semantor* are also fused at the proximal epiphysis, as they are in extant pinnipeds (Berta and Wyss, 1994). While *Semantor* has been interpreted as phocid-like in general dimensions, it displays a suite of features that more closely resembles otarioids, desmatophocids, and stem pinnipeds. Biomechanical reconstructions of *Semantor* are futile owing to its incompleteness.

Remarks on the auditory region in pinnipeds

Greater scrutiny of the auditory region of pinnipeds, including the middle ear and the inner ear, contributed significantly to a reinterpretation of their phylogenetic relationships (Wyss, 1987; 1988; Berta and Wyss, 1994). The auditory region of *Puijila darwini* does not closely resemble that of any extant aquatic or semi-aquatic Carnivoran. Rather, it closely approximates that of *Enaliarctos* (Mitchell and Tedford, 1973; Berta, 1991; Cullen et al., 2014).

Mitchell and Tedford (1973) reported of a low horizontal septum across the anterior portion of the bulla in LACM 4321, the holotype skull of *Enaliarctos mealsi*. A similar septum is also reported in *Pinnarctidion bishopi* (Barnes, 1979), but is not visible in USNM 314325 (*Pinnarctidion rayi*). NUFV-405 and USNM-314290 (*Enaliarctos emlongi*) display nearly identical intrabullar septae (Figure 1.24), similar in appearance to that described by Mitchell and Tedford (1973). However, the septae in these skulls are thick and traverse the bullar chamber at an oblique angle, stretching from the carotid to a point just dorsolateral to the probable entotympanic-ectotympanic junction. Among

caniforms studied, this specific configuration appears uniquely shared between *Puijila*, *Enaliarctos mealsi*, *Enaliarctos emlongi*, and possibly *Pinnarctidion* (Barnes, 1979). It is not observed in the extant pinnipeds or later-diverging pinnipedimorphs (Present Study; Deméré and Berta, 2002).

In general, bullar septae are widely distributed in caniforms, but many of these septae do not appear to be homologous with the low anterior septum of *Puijila*, *Enaliarctos* and *Pinnarctidion*. canids typically display a low septum across the entotympanic-ectotympanic junction (Wang, 1994). This septum is found even in fossil forms (Wang, 1994), though it varies in its shape and its continuity across the bullar chamber (Ivanoff, 2006). *Prohesperocyon* – the earliest-diverging canid – does not bear such a septum (Wang, 1994), suggesting the canid septum is uniquely derived. The septum of *Canis* is ostensibly formed wholly by the caudal entotympanic (Hunt, 1974), differing from the felid and viverrid condition, in which a long septum is formed by the inflection of both tympanic and caudal entotympanic. Furthermore, the felid septum displays a foramen and is responsible for a notch (loss of hearing) at a frequency within the range of 2-4kHz. The felid and viverrid condition has been referred to as a true bullar septum, with those observed in canids and mustelids deemed ‘pseudoseptae’ (Hunt, 1974). Various mustelids, including fossils forms, display radiating septae, occasionally so pronounced as to be visible on the external surface of the bullae (Hough, 1948). *Lontra canadiensis* displays a very weak horizontal septum, but its position and its connection to surrounding elements differ markedly from that of *Puijila* (Figure 1.24). Most notably the ventral chamber arises before the dorsal chamber in *Lontra*.

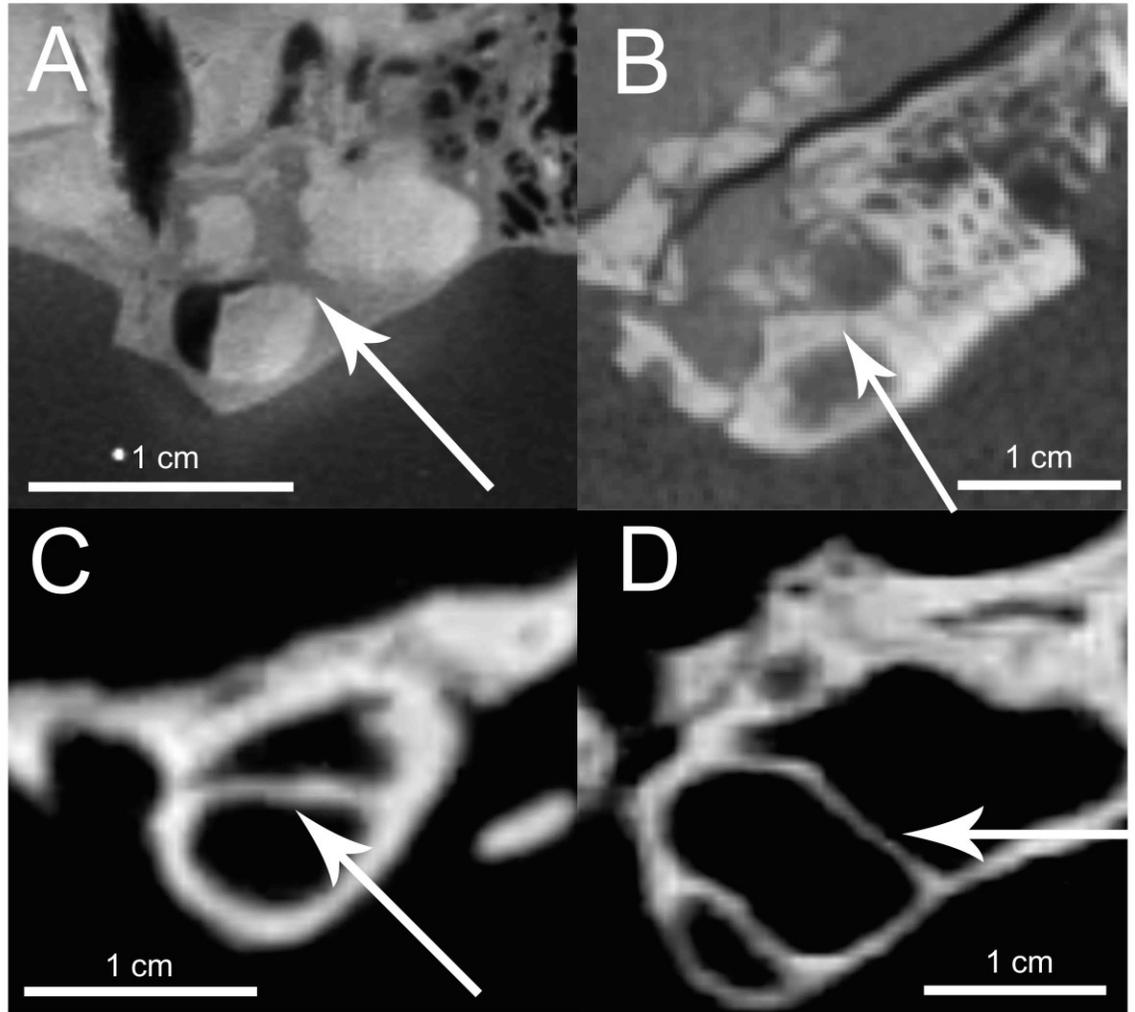


Figure 1.24. Coronal slices taken from HR μ CT data displaying intrabullar septum in selected specimens: A. NUFV-405 (*Puijila darwini*). B. USNM 314290 (*Enaliarctos emlongi*) C. digimorph.org/specimens/Gulo_gulo/Male (*Gulo gulo*). Arrow points to intrabullar septum. Figure of *Puijila* is left bulla flipped horizontally to showcase better preserved side.

It is unlikely the similar appearance of the septum in *Puijila* and *Enaliarctos* represents convergence of a feature functionally relevant to a semi-aquatic lifestyle. No other semi-aquatic taxa, within or outside of the pinniped radiation (excepting *Pinnarctidion*), display such a septum, including *Potamotherium* (Mitchell and Tedford, 1973). The function of this intrabullar septum is unknown. Huang et al. (2000) suggest

the felid intrabullar septum, and its associated foramen, may supplement the bullar wall to provide additional mechanical strength. Furthermore, the septum may reduce undesirable features of the middle ear response (e.g., wave effects in the cavities) that threaten to interfere with sound localization (Huang et al., 2000;2002). Such a function appears unnecessary for organisms adapted to an aquatic existence, suggesting its appearance in pinnipedimorphs may represent the maintenance or vestigial retention of a terrestrial adaptation in taxa that may have still spent a significant amount of time on land. However, extant phocines, monachines, and otariids appear to be excellently capable of localizing aerial sounds (Holt et al., 2004; 2005). This auditory proficiency is possibly related to communication across a large breeding colony. It may be retained even in those pinniped taxa that do not form colonies as strong polygyny is thought to characterise the base of Pinnipedia (Cullen et al., 2014). Investigation of the middle ear of additional stem arctoids, through the use of HR μ CT, may reveal the timing of the origin and subsequent loss of the intrabullar septum, which can now be considered a potential pinnipedimorph synapomorphy.

The configuration of the auditory bulla has frequently been used to differentiate between major lineages of carnivorans (Hunt, 1974), though the types do not neatly align with phylogenetic hypotheses. *Puijila* displays an inflated and rounded auditory bulla, with a slightly greater contribution from the ectotympanic and a rounded posterior margin. A similar bulla is observed in *Enaliarctos mitchelli*, *Enaliarctos mealsi*, and *Pteronarctos godertae*. The bullae of *E. tedfordi*, *E. emlongi* and *Potamotherium* are less inflated, do not appear rounded in lateral or medial view, and display a straight or convex posterior margin, resulting in a triangular shape in ventral view. *Potamotherium* and *E.*

tedfordi also display a small, medially-folded flange on the ventral surface of the bulla, at the junction between the carotid canal and the rostral entotympanic, absent in *Puijila*, *E. mitchelli*, and *E. mealsi*. The entotympanic of *Enaliarctos mealsi* displays a similar ratio of entotympanic-to-ectotympanic, though the entotympanic is somewhat more expanded (Tedford, 1976). *Potamotherium* has been described as possessing an entotympanic dominated bulla (Tedford, 1976), though the contribution does not appear to depart significantly in that direction compared to those of *Puijila* or *Enaliarctos* (Personal Obs.).

Phylogenetic significance has also been conferred upon the presence of a tubular auditory meatus, and its amount of lateral expansion (Hunt, 1974; Wolsan, 1993). The meatal trough of *Puijila* is long relative to the bullar portion housing the tympanic cavity, covering all but a sliver of the external auditory meatus. The meatal trough of *Potamotherium* is anteroposteriorly broader, less laterally extensive, and less obliquely oriented than that of *Puijila*.

A significantly embayed lateral margin of the basioccipital in *Puijila* is undoubtedly a retention of a primitive feature. This feature was likely present at the base of Arctoidea, as it appears in the earliest members of the Caniformia (Tomiya and Tseng, 2016). A deep basioccipital embayment has been identified in Amphicyonids, ursids and their ancestors, and pinnipedimorphs (Hunt and Barnes, 1994). In these taxa, the dorsal and ventral arms of the basioccipital and the medial portion of the petrosal circumscribe the inferior petrosal sinus, which is known to house a double loop of the internal carotid artery in many extant ursids. A shallow embayment, with prominent dorsal and ventral arms encapsulating a small sinus, is found in an early mustelid (Paterson et al., In prep). *Gulo*, the largest extant terrestrial mustelid, has independently evolved a subdural loop

for the internal carotid artery (Hunt and Barnes, 1994). However, that of *Gulo* lies in the cavernous sinus and the inferior petrosal sinus is absent. Due to its large body size, *Gulo*, like ursids and Amphicyonids, likely has more trouble dissipating heat than smaller mustelids. A looped carotid artery prolongs the cooling time of blood flowing brainward. Such a mechanism is unnecessary for aquatic taxa (Hunt and Barnes, 1994), and has expectedly been lost in derived pinnipeds. The timing of this loss is not well-understood, but likely occurred independently in the three extant pinniped families, as suggested by its retention in early-diverging odobenids.

The round window of *Puijila* is nearly twice the size of the oval window. While a comparative scan of *Potamotherium* is unavailable, it appears the round window-to-oval window ratio is comparable to that of *Puijila*. An enlarged round window is not exclusive to pinnipedimorphs (Decker and Wozencraft, 1991). However, *Puijila* and *Potamotherium* also display an incipient round window fossula, a feature only observed in pinnipeds and some lutrines among carnivorans (Wyss, 1987).

Peculiarly, pinnipeds display contrasting patterns of semicircular canal configuration. Phocids have a larger arced canal system than terrestrial carnivores, expected given their remarkable agility (Spoor and Thewissen, 2008). Contrarily, otariids possess less arced anterior and posterior canals, suggesting a reduction in mechanical sensitivity, a detail that is difficult to reconcile with their acrobatic swimming kinematics. A synapomorphy of phocids is a transversely-oriented basal whorl of the cochlea (Wyss, 1987; 1988). The erect basal whorls of otariids and *Odobenus* are oriented similarly to those of terrestrial carnivorans (Berta and Wyss, 1994). Though the basal whorl of *Puijila*

departs from the plesiomorphic condition, a great tract separates it from the specialized configuration observed in phocids.

Remarks on the dentition of pinnipedimorphs

The heterodont dentition of *Puijila* is accordant with the hypothetical condition at the base of pinnipeds, deviating only slightly from the condition at the base of arctoids, exemplified by *Amphicticeps*, *Cephalogale*, and *Mustelavus*. Reflecting its transitional status, the molars of *Puijila* experience a reduction relative to these other early-diverging arctoids, a trend continuing in later-diverging pinnipedimorphs, whose molars are further reduced, and eventually lost altogether (Berta and Wyss, 1994; Boessenecker and Churchill, 2013). Early-diverging mustelids also display a reduction in the size of the molars, but *Puijila*'s retention of a postprotocrista and its lack of a lingual notch on the talonid of its M₁ firmly exclude it from Mustelidae. The posterolingual placement of M² connects *Puijila*, *Potamotherium*, and *Enaliarctos*, and has been suggested to represent a pinniped synapomorphy (Wolsan, 1993). However, this placement may be caused by crowding reflecting shortening of the tooth row, and also appears in *Amphicticeps* (Wang et al., 2005) and *Megalictis* (Valenciano et al., 2016).

Rybczynski et al. (2009), in an abridged/preliminary phylogenetic analysis, recovered a clade of amphicyodontines as the sister group to pinnipeds. The Amphicyodontinae are represented by *Allocyon*, *Kolponomos*, *Pachycynodon*, *Amphicynodon*, and possibly *Amphicticeps* (Tedford et al., 1994; Hunt, 1998). Rybczynski et al. (2009) recovered *Amphicticeps* along the pinniped stem, as sister to a group of *Enaliarctos*, *Puijila*, and *Potamotherium*. The phylogenetic position of

Amphicticeps has been difficult to pin down (Wang et al., 2005), owing to its generally primitive morphology. Its placement along the pinniped branch group is suggested by just a pair of characters of dubious phylogenetic utility – a long postorbital constriction, and a lingually-displaced M². Both these characters appear homoplastically in some crown mustelids, and the length of the postorbital constriction appears intermediary between ‘fissipeds’ and pinnipedimorphs. This suite of characters, in conjunction with others thought to ancestrally characterise arctoids and stem pinnipeds, (eg., presence of an inferior petrosal sinus) make it difficult to establish an intimate relationship between *Amphicticeps* and pinnipedimorphs, though further material of *Amphicticeps* may confirm its pinnipedimorph affinities.

Results of the Biomechanical Analysis

Using the predictive power of the PCA of Bebej (2009), *Puijila* is identified as well-adapted for aquatic locomotion, and as a forelimb-dominated swimmer. These results are visualized in Figure 1.25. *Puijila darwini* is identified as better aquatically-adapted than any extant otter, and nearly as specialized for forelimb-dominated locomotion as some extant otariids. *Potamotherium* was identified as slightly less aquatically-specialized compared to *Puijila*, and was identified as a slightly forelimb-dominated swimmer, though closer on that axis to some extant phocids than extant otariids.

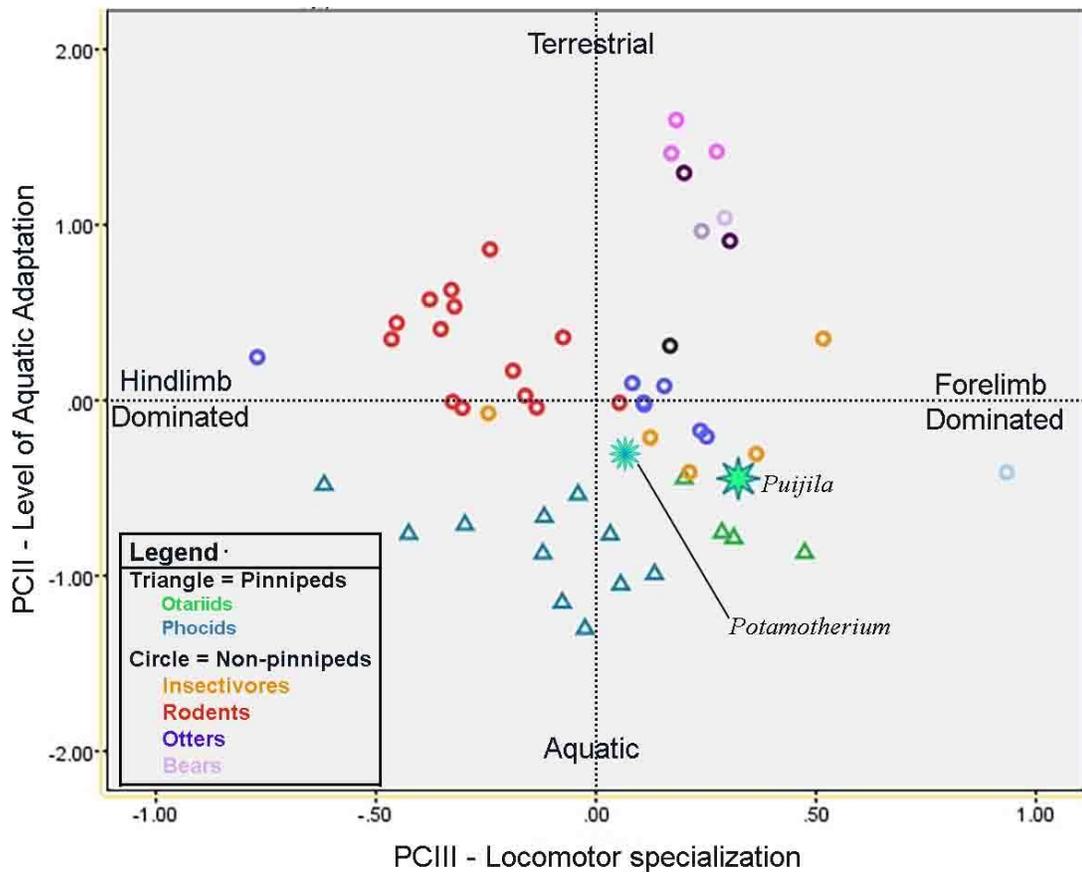


Figure 1.25. Results of principal components analysis from Bebej (2009), modified to display PC2 and PC3 scores for *Puijila darwini* and *Potamotherium valetoni*.

Following Samuels et al. (2013), stepwise DFA of locomotor categories was performed with the functional indices for the extant species and the unclassified extinct carnivorans. Eight of the 16 indices were included in the stepwise discriminant model (Table 6). Six discriminant functions were employed in the analysis. The first two discriminant functions both had eigenvalues over one and accounted for a combined 77.8% of the total variance. The DFA separated groups fairly well (Wilks' lambda=0.036, P=0.000), though there was substantial overlap between groups,

understandable as the simplified categories, for the sake of this analysis, do not wholly represent the continuum of locomotory modes displayed across carnivorans.

The first discriminant function (DF1) accounted for 56.2% of the variance, and displayed an eigenvalue of 3.283. DF1 primarily discriminated between terrestrial and aquatic forms. DF1 was positively correlated with humeral epicondylar index (HEI), femoral epicondylar index (FEI), and pes length index (PES), and negatively correlated with tibial robustness index (TRI), claw length index (CLAW), and manus proportions index (MANUS).

The second discriminant function (DF2) accounted for 21.5% of the variance, and displayed an eigenvalue of 1.255. DF2 primarily separated the generalist and cursorial from the semifossorial groups. DF2 was positively correlated with PES, TRI, and intermembral index (IM), and negatively correlated with tibial spine index (TSI) and CLAW.

The classification phase was used to assess the ability of the discriminant model to separate species into locomotor groups. With regards to the extant Carnivoran species in the analysis, 66.3% of were correctly classified. The analysis was accurately able to classify arboreal, cursorial, semifossorial, and hindlimb-dominated aquatic groups (all >80% correct classifications), while generalist and forelimb-dominated aquatic taxa were not very accurately classified (40.7% and 50% correct, respectively). While there was overlap between the forelimb-dominated aquatic and hindlimb-dominated aquatic taxa, no taxa from either group was inappropriately allocated to the other aquatic group, nor were they misclassified in the semi-fossorial group.

Potamotherium was not complete enough to be included as an unknown in the classification phase of the analysis. *Puijila darwini* was complete enough to include, as were seven other fossil taxa. *Puijila darwini* was classified as hindlimb-dominated aquatic in this analysis. Its second most likely group was forelimb-dominated aquatic. However, it was further from its group centroid than every extant taxon in the analysis (Squared Mahalanobis Distance=18.88), and every extinct taxon excepting *Smilodon fatalis*. *Puijila* plotted close to the extant otariids in the analysis, but was far from the other forelimb-dominated swimmers in the analysis. A scatter-plot of the DF1 and DF2 scores for all taxa included in the analysis is presented in Figure 1.26.

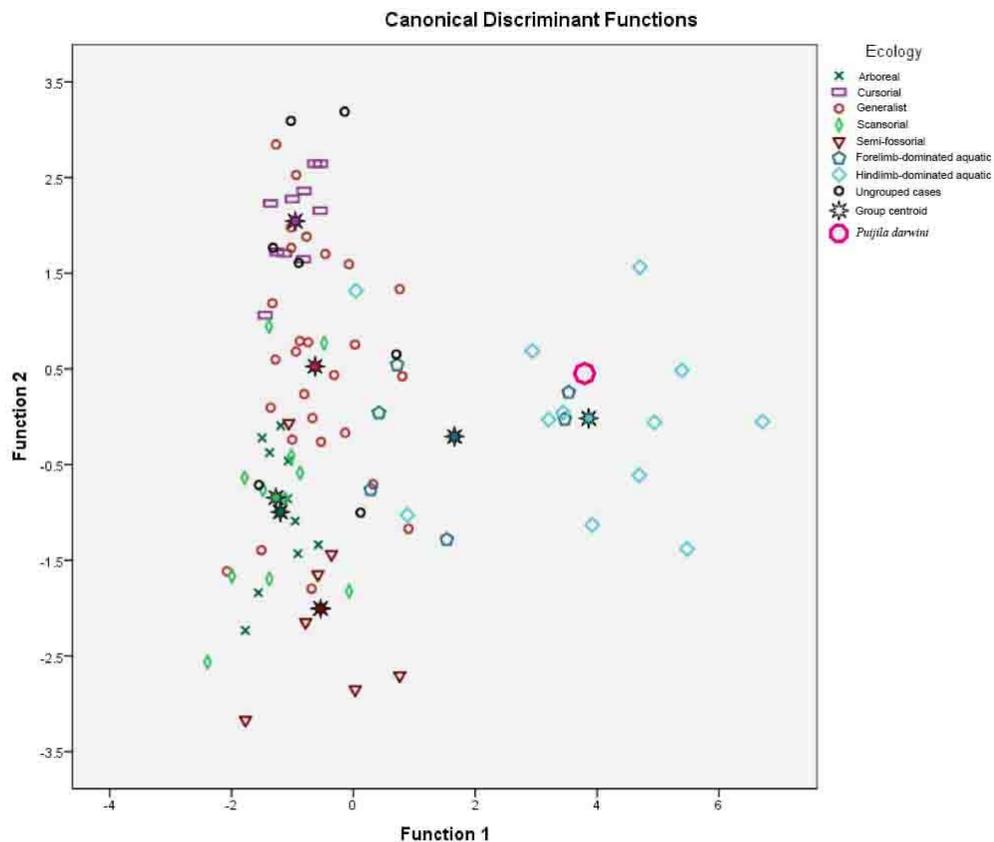


Figure 1.26. Plot of DF1 and DF2 scores for analysis of locomotor groups.

Discussion

Pinnipeds are frequently excluded from biomechanical analyses of terrestrial or semi-aquatic carnivorans (Van Valkenburgh, 1987; Taylor, 1989; Janis and Wilhelm, 1993; Samuels et al., 2013). Their extreme aquatic adaptations, reflected in their morphology, are thought to both obscure their phylogenetic position and produce disorder in analyses investigating more nuanced changes in terrestrially-adapted taxa (Bininda-Emonds and Gittleman, 2000). However, the exclusion of pinnipeds from such studies conceals the evolutionary and adaptive significance of pinniped biology, masking details of the aquatic transition. Furthermore, the work of Bininda-Emonds et al. (2000) suggests the adaptive differences between aquatic and terrestrial carnivorans are no more numerous or significant than those between other ecomorphological groups, rendering the a priori assumption - that pinnipeds will make such studies intractable - dubious. Ignoring organisms that deviate from the norm may improve precision, but risks making a sample paraphyletic, and the conclusions incomplete.

The discriminant function analysis of Samuels et al. (2013) operated within the confines of “fissipedia”, excluding pinnipeds. This analysis was able to accurately discriminate between carnivoran taxa occupying six different locomotory groups, but excluded fully-aquatic pinnipeds. In the present study, with pinnipeds added, the DFA retained its ability to discriminate between these groups, but was also capable of discriminating between aquatic and semiaquatic taxa displaying either forelimb-dominated locomotion or hindlimb-dominated locomotion. The DFA was particularly adept at classifying hindlimb-dominated aquatic taxa, while forelimb-dominated taxa

were occasionally misclassified (Table 7). *Puijila darwini* was classified as hindlimb-dominated in this analysis, though the drastic distance between its DF scores and the group centroid are concerning. *Puijila* scored highly on DF1, as did pinnipeds and other aquatic taxa. The three indices associated with a high DF1 score relate to the expanded femoral and humeral condyles observed in aquatic taxa (FEI and HEI) and an expansion in digit size accompanying a reduction in longbone size (PES). *Puijila*'s second most likely group was forelimb-dominated aquatic, though it fell well outside of the range of other forelimb-dominated semi-aquatic taxa (except for extant otariids), who, when misclassified, were not identified as hindlimb-dominated aquatic. These results confirm the aquatic adaptations of *Puijila*'s postcranial skeleton, with slightly more support for hindlimb-dominated locomotion, but these results do not confidently identify its mode of aquatic propulsion.

The initial PCA of Bebej (2009) is more germane to the discussion of the plesiomorphic swimming condition in pinnipeds. This analysis was performed within the context of all semi-aquatic mammals analyzed, including a higher proportion of pinnipeds than included in the original analysis of Gingerich (2003). As *Puijila* is ostensibly less aquatically-adapted than any known pinniped, its swimming behaviour may not be specialized enough to investigate it within the dichotomy presented by extant pinnipeds.

Superficially, the postcranial skeleton of *Puijila* is most similar to that of the extant river otters. However, *Puijila* displays a bulkier bauplane than the ectomorphic designs of the lutrines. *Puijila*'s longbones rival those of *Gulo* in terms of robusticity, displaying broad and sharp muscular attachment sites and well-defined muscle scarring.

Proportionally, the relative length of *Puijila*'s long bones are in line with those of other semi-aquatic carnivorans (Rybczynski et al., 2009supp).

Subjecting NUFV-405 to the PCA of Bebej (2009), it can be observed that *Puijila* deviates significantly from lutrines on the second and third principal components, which represent degree of aquatic adaptation, and degree of forelimb vs hindlimb dominated swimming, respectively. NUFV-405's score for the second principal component suggest *Puijila* was well-adapted to an aquatic existence, even moreso than *Potamotherium*, a notion belied by *Puijila*'s long limbs. NUFV-405's positive scores on the third principal component suggest it likely engaged in forelimb-dominated locomotion, a notion further supported by the long deltopectoral crest of the humerus, which is also elongated in otariids. Such a scenario would be discordant with previous views of the plesiomorphic swimming condition in pinnipeds, which have envisioned a swimming style utilising both fore- and hind-limb dominated apparatuses (Berta and Ray, 1990; Furbish, 2015). Such a swimming style is unknown in any extant semi-aquatic mammal. While it is conceivable such a non-partisan swimming style may define the hypothetical last common ancestor of pinnipeds, it does not conform well with models that attempt to reconstruct the evolution of aquatic locomotion in extant lineages (Fish, 1996; Kuhn and Frey, 2012).

Fish (1996, 2000) developed a model to explain the possible sequence of locomotory and morphological transitions resulting in the lift-based propulsion performed by Cetaceans, Sirenians, and pinnipeds. All of these lineages are derived from fully terrestrial taxa, and thus, must have initially engaged in quadrupedal paddling during their occasional forays into water (Fish, 2016). Such "doggie" paddling is employed by quadrupedal mammals (Davis, 1942), who are constrained by the

neuromotor patterns associated with a quadrupedal terrestrial gait (Smith, 1994).

Paddling using paired appendages to produce drag is not efficient, necessitating locomotory specializations in taxa who commit further to an aquatic environment.

Semi-aquatic mammals tend to retain drag-based paddling when swimming at the surface, but improve mechanical efficiency in the water by restricting propulsion to either their forelimbs or hindlimbs. This frees the unengaged pair of limbs for other uses, including prey capture and stabilisation. Such bipedal paddling involves alternate strokes of either the pectoral or pelvic limbs, and is typically associated with skeletal changes, including an elongation of the digits and a shortening of the humerus and femur (Fish, 2016). Among extant mammals, pectoral paddling is observed in the polar bear (*Ursus maritimus*) (Williams and Worthy, 2002) and the ferret (*Mustela putorius*) (Fish and Baudinette, 2008), and pelvic paddling is displayed by muskrats and desmans (Gingerich, 2003). The energetic cost of being a semi-aquatic mammal, not remarkably well-adapted for land or water, is higher than the cost of being purely terrestrial or purely aquatic (Williams, 1999). Expectedly, a semi-aquatic stage has served as a transitory stage in the evolution of all aquatic mammals, with further aquatic specializations common in taxa who have taken the plunge into the sea.

Further aquatic specialization, beyond drag-based surface paddling, typically necessitates more drastic changes in anatomy and neurology. In his model, Fish (2016) suggests commitment to a paddling stroke that excludes one set of limbs constrains the type of locomotion a semi-aquatic mammal can engage in when submerged. If an organism becomes adapted to foraging underwater, favouring of the pectoral limbs will ostensibly result in further modifications to accommodate simultaneous pectoral rowing,

as observed in the platypus (Howell, 1929). Likewise, a preference for pelvic paddling is likely to usher a shift to alternate pelvic rowing, though it may also lead to simultaneous pelvis paddling (Fish, 2016). Rowing demands the humerus or femur is abducted to the horizontal plane. This reorientation is necessary for counteracting positive buoyancy. To accommodate this reorientation, further osteological modifications are warranted, causing the rowing mammal to further depart from a terrestrial morphology, ejecting it from a compromised position between taxa specialized for a terrestrial existence and those better-equipped for an aquatic lifestyle.

Most derived aquatic mammals further abandon their terrestrial adaptations by modifying their propulsive appendages into wing-like hydrofoils to produce lift. Ostensibly pectoral paddlers develop pectoral oscillation as a means of producing thrust, as in otariids, and pelvis paddlers evolve pelvic oscillation, exemplified by phocids. Compensating for body mass and degree of aquatic specialization, it is observed that the trunk and limb proportions of pectoral oscillators are not wholly dissimilar to those of pectoral paddlers or rowers, and the same relationship holds true for pelvic oscillators and pelvic rowers/paddlers (Gingerich, 2003).

It is difficult to integrate pinnipeds into the model formulated by Fish (1996, 2000, 2016). *Odobenus* is particularly problematic. Though it employs its large paddle-like forelimbs to produce thrust at low speeds, the pelvic region is more crucial to its movement, as it is engaged during more energetic bouts of locomotion (Gordon, 1981). Preference for pelvic oscillations is unexpected given Fish's model as odobenids are believed to share a common ancestor with otariids, who display pectorial oscillations (Flynn et al., 2005; Fulton and Strobeck, 2007). Within the framework of Fish,

independent acquisitions of aquatic specializations appear plausible to describe the discrepant locomotory modes in otariids and phocids, but this notion is contradicted by the locomotory mode observed in the highly autapomorphic *Odobenus*. The plesiomorphic swimming style for odobenids is unknown, and there are no known complete skeletons for any early-diverging walruses.

Furthermore, Fish (2016) found it difficult to accommodate the long tails of *Puijila* and *Potamotherium*, as a long tail would be expected to be reduced in semi-aquatic mammals that employ their pectoral or pelvic apparatus to produce thrust. However, at this stage in the aquatic transition, selective pressures favouring a decrease in tails size may have yet to strongly assert themselves.

Nevertheless, the PCA identifies *Puijila* as well aquatically-specialized, moreso than any living lutrine and approaching some otariid and phocid taxa. Unfortunately, the present analyses disagree on the precise locomotory specialization likely employed by *Puijila*, making it difficult to use *Puijila* to assess the plesiomorphic swimming condition of pinnipeds. The lack of resolution of these analyses suggests the aquatic transition or transitions of pinnipeds do not neatly fit into preconceived models of aquatic adaptation (Fish, 2016).

Conclusion

The dichotomous phylogenetic relations between otarioids and phocids have obscured details of their aquatic transition. These two groups also lack conspicuous transitional forms, as the earliest known fossil phocids and fossil otariids with postcrania available already appear very specialized (Deméré and Berta, 2005; Rahmat and

Koretsky, 2016). Previous studies attempting to reconstruct the locomotory modes of *Enaliarctos* have been in disagreement with each other, making it difficult to infer the plesiomorphic swimming condition in pinnipeds. The two biomechanical proxies in the present study agree that *Puijila* is well aquatically-adapted, but also disagree on its specific locomotory specialization. A greater understanding of the poorly understood aquatic transition in pinnipeds must await more complete postcranial skeletons of fossil pinnipeds.

Chapter 3: A total evidence phylogenetic analysis of pinniped phylogeny; the possibility of parallel evolution within a monophyletic framework

Abstract

In the present study, a series of phylogenetic analyses of morphological, molecular, and combined morphological-molecular datasets were conducted to investigate the relationships of 23 extant and 44 fossil caniforme genera, in order to test the phylogenetic position of putative stem pinniped *Puijila* within a comprehensive evolutionary framework. With *Canis* as an outgroup, Bayesian inference of the combined dataset recovered a topology in which musteloids serve as the sister group to a monophyletic pinniped lineage, to the exclusion of ursids, and recovered *Puijila* as sister taxon to *Potamotherium* within the pinniped divergence. Similar results were obtained from Bayesian analyses of a Total Morphology data set, a Craniomandibular Only data set, a Craniomandibular + Dental Only data set, and a Postcranial Only data set, and Parsimony analyses of the Total Morphology and Craniomandibular + Dental Only data set. However, the different analyses did not agree on the sister group to pinnipeds, with molecular and total evidence analyses favouring musteloids, and morphological analyses favoring mustelids or ursids. Furthermore, while the total evidence analysis and molecular analyses recovered a closer association between otariids and odobenids, the Bayesian analyses of morphological datasets preferred a closer relationship between otariids and phocids. While the phylogenetic analyses did not directly provide any evidence of parallel evolution within the pinniped extant families, it is apparent from the

inspection of previously-proposed pinniped synapomorphies, within the context of a molecular-based phylogenetic framework, that many traits shared between extant pinnipeds have arisen independently in the three lineages. Notably, those traits relating to homodonty and limb-bone specialization (for an aquatic lifestyle) appear to have multiple origins within the crown group, as suggested by the retention of the plesiomorphic conditions in early-diverging fossil members of the three extant families. Parallel evolution may not bear itself out in phylogenetic analyses of morphological data due to the limitations associated with the Mk model of Bayesian inference.

Introduction

From the 1960's until the late 1980's, pinnipeds were widely believed to be diphyletic, based partly on the divergent locomotory styles and morphologies observed in extant taxa (McLaren, 1960; Tedford, 1976; Ray, 1976; Repenning and Tedford, 1977; de Muizon, 1982a, 1982b; Wozencraft, 1989; Nojima, 1990). A diphyletic view aligns phocids with musteloids (a clade containing mustelids, procyonids, ailurids, and mephitids), and grouped otarioids (otariids and odobenids) with ursoids (bears) (Figure 2.1). The paradigm shifted when Wyss (1987) provided evidence from inner ear morphology strongly suggesting a monophyletic relationship of phocids, otariids, and odobenids (Figure 2.2). Wyss' careful observation of this anatomy and subsequent recognition of pinniped homologies corroborated earlier biochemical work identifying pinnipeds as monophyletic (Arnason, 1974; Romero-Herrera et al., 1978; de Jong and Goodman, 1982; Miyamoto and Goodman, 1986). From the publication of Wyss (1987) to the present, the vast majority of phylogenetic studies have confirmed Wyss' assertion,

regardless if the nature of the evidence was molecular (Fulton and Strobeck, 2006; Flynn et al., 2005; Sato et al., 2006; Yonezawa et al., 2009), morphological (Berta and Wyss, 1994; Demere and Berta, 2002; Kohno, 2006; Furbish, 2015), or a combination of the two (Flynn et al., 2000). However, some morphological (Koretsky et al., 2016), biomechanical (Kuhn and Frey, 2012) and biogeographical (Koretsky and Barnes, 2006) studies continue to uncover evidence questioning the monophyly of pinnipeds, though these studies disregard the wealth of molecular evidence in support of monophyly.

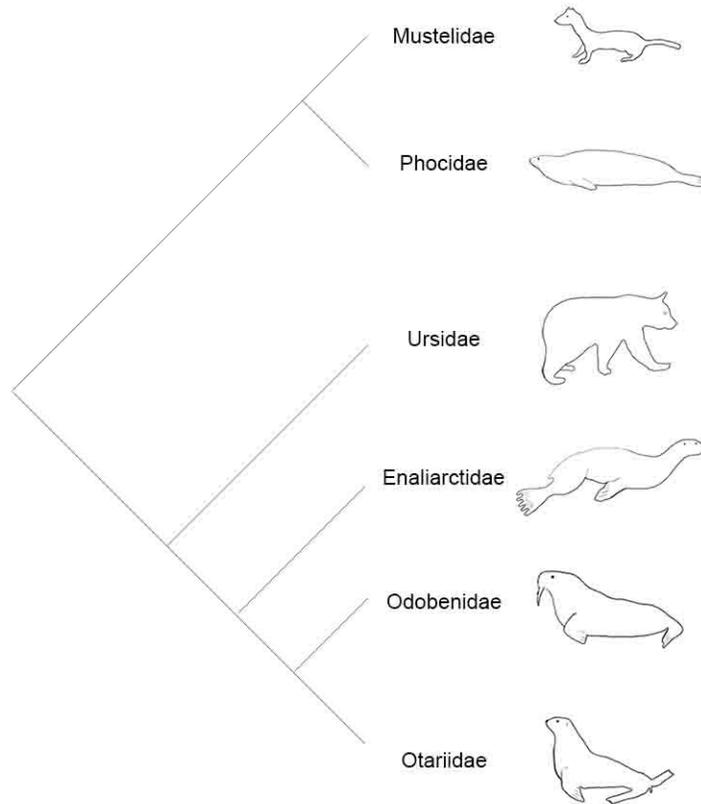


Figure 2.1. Hypothesis of the evolutionary relationships of arctoids under a diphyletic view.

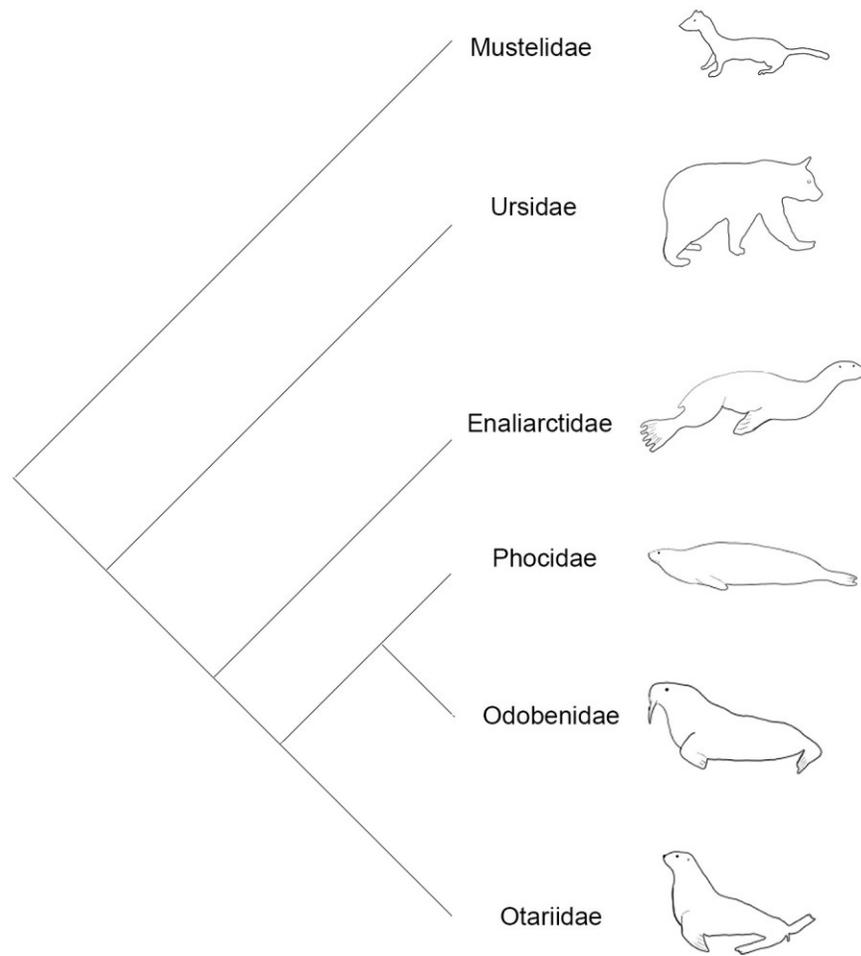


Figure 2.2. Hypothesis of the evolutionary relationships of arctoids under a monophyletic view, based on morphological evidence (Wyss, 1987; Berta and Wyss, 1994).

Though pinniped monophyly has been well-supported by both molecular and morphological data, it is not apparent how phocids and otariids developed such disparate morphologies and locomotory modes. A diphyletic origin of pinnipeds serves as a compelling argument to explain the contrasting swimming styles and morphological disparity observed between otariids and phocids (Kuhn and Frey, 2012). Otariids are

more ursid-like in general appearance and retain the capability of inverting their hindlimbs on land, allowing them to perform some semblance of quadrupedal ambulatory locomotion (Berta, 2012). When submerged, otariids engage in pectoral oscillations, using their enlarged foreflippers to figuratively fly through the water (English, 1976b). The more fusiform phocids are unable to revert their hindlimbs forward on land, and swim using pelvic oscillations, producing thrust underwater via horizontal undulations of their pelvic region and alternate protraction and retraction of their hindflippers (Fish et al., 1988; Pierce et al., 2011). The highly autapomorphic *Odobenus rosmarus*, the lone extant member of the once speciose Odobenidae, is not easily accommodated into either group. *Odobenus* is more otariid-like in general appearance, but shares a peculiar suite of features with phocids, not found in otariids (Wyss, 1987; Berta and Wyss, 1994). *Odobenus* displays an intermediary swimming style, using pectoral oscillations at slow speeds and pelvic undulations at high speeds (Gordon, 1981). Fossil evidence led diphyletic proponents to identify it as a highly-derived otarioid, a notion supported by molecular studies, though not within the framework of a diphyletic Pinnipedia (Flynn et al., 2000; Fulton and Strobeck, 2007).

The evolutionary relationships advocated by proponents of pinniped diphyletic were not subject to the rigor of cladistics. Rather, proponents of pinniped diphyletic invoked a small number of phylogenetically-significant features shared between otarioids and ursids on the one hand, and phocids and mustelids on the other hand (MacLaren, 1960; Tedford, 1976; de Muizon, 1981). The features shared between otarioids and phocids, largely in the postcranial skeleton and auditory region, were disregarded due to their perceived susceptibility to homoplasy (Tedford, 1976), a notion later shown to be untenable within

a phylogenetic framework (Wyss, 1987; 1988). Cladistic analyses of large morphological datasets have unilaterally supported pinniped monophyly (Berta and Wyss, 1994; Furbish, 2015). However, such analyses have had difficulty establishing the relationship of pinnipeds to other arctoids, as their results are typically incongruent with the relationships identified by molecular analyses (e.g., Berta and Wyss, 1994 vs Fulton and Strobeck, 2007). This problem is exacerbated by the paucity of fossil remains representing early-diverging pinnipeds that could fill in the gap between them and any putative arctoid clade (Deméré et al., 2003).

Since the establishment of pinniped monophyly (Wyss, 1987, 1988; Berta et al., 1989), the most contentious issue in pinniped systematics has been the placement of pinnipeds within Arctoidea. Phylogenetic analyses of morphological data are in disagreement over the sister group of pinnipeds, with musteloids and ursids both presenting compelling cases. Identification of Ursidae as the sister group to pinnipeds was a minor component of early hypotheses of pinniped monophyly (Wyss, 1987; Berta and Wyss, 1994), as the most recent common ancestor of pinnipeds was envisioned as ursid-like. *Enaliarctos*, the earliest-diverging pinnipedimorph known at the time, possesses many features which were thought to characterize ursids ancestrally, including a shelf-like P⁴ protocone, a labiolingually-restricted M¹, and a deep lateral basioccipital embayment for the inferior petrosal sinus (Mitchell and Tedford, 1973; Flynn et al., 1988; Hunt and Barnes, 1994). However, Wolsan (1993) and Kohno (1993, 1994, 1996) recovered musteloids as the sister group to pinnipeds, a pairing strongly supported by molecular data (Figure 2.3) (Flynn et al., 2005; Fulton and Strobeck, 2007; Sato et al., 2009; Sato et al., 2012).

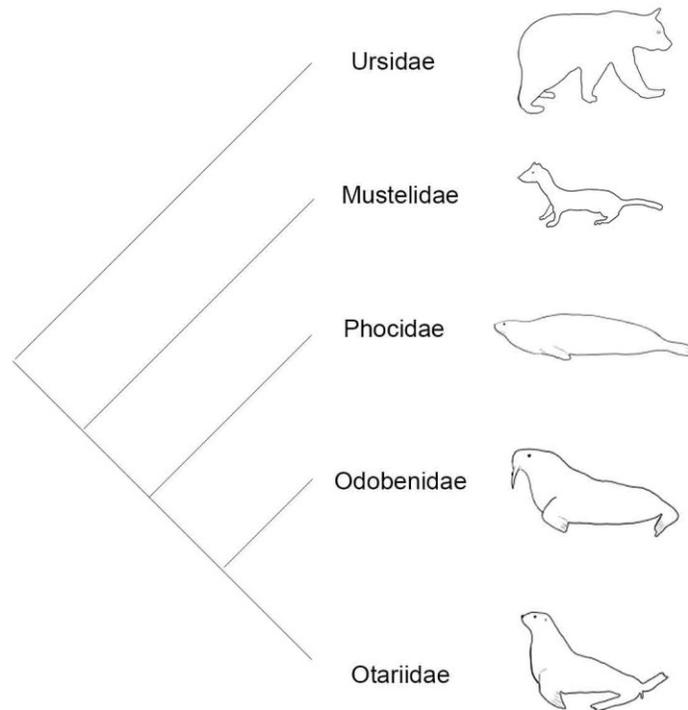


Figure 2.3. Hypothesis of the evolutionary relationships of arctoids based on cladistic studies of molecular data (Flynn et al., 2005; Fulton and Strobeck, 2007; Sato et al., 2009).

Puijila darwini, uncovered from lacustrine deposits in the High Arctic, was originally proposed to be a transitional pinniped (Rybczynski et al., 2009), filling in the gap between the fully-flipped *Enaliarctos* and terrestrial carnivorans. This hypothesis was based on a parsimony analysis, employing exclusively morphological characters, investigating the relationships of *Puijila* to terrestrial and semi-aquatic arctoids. However, this interpretation requires a more comprehensive phylogenetic analysis (Diedrich, 2011; Berta, 2012; Boessenecker and Churchill, 2013; Koretsky and Domning, 2014; Koretsky et al., 2016). In the initial analysis (Rybczynski et al. 2009), *Puijila* was recovered in a clade with *Enaliarctos*, *Potamotherium*, and *Amphicticeps*, thereby

supporting the notion *Puijila* is either a pinniped, a pinnipedimorph, or an earlier-diverging member of this lineage. However, an extensive sampling of crown-group pinnipeds was not included. Thus, a hypothesis of its precise relationship to pinnipeds requires a phylogenetic analysis inclusive of additional pinnipeds beyond *Enaliarctos*.

Many phylogenetic analyses of arctoids have problematically excluded pinnipeds (Bininda-Emonds and Gittleman, 2000), under the assumption the extreme aquatic adaptations of derived pinnipeds may obscure their relationships to terrestrial arctoids. Moreover, analyses investigating the interrelationships of pinnipeds and other arctoids have been limited to extant/crown taxa. Morphological analyses have included only broadly-defined “Mustelidae”, “Ursidae”, and/or “Amphicyonidae” as outgroups (Berta and Wyss, 1994; Kohno, 1993, 1994). Attempting to assimilate in-group taxa into a hypothetical common ancestor is indeed more prudent than using exemplary taxa (Bininda-Emonds et al., 1998b), but still requires many assumptions (e.g., monophyly), which can be easily violated by incompletely preserved fossil taxa.

Excepting Finarelli (2008), which included only a single pinniped species, phylogenetic analyses of fossil arctoids have omitted extant taxa (Wolsan, 1993; Wang et al., 2005). Such analyses have provided valuable insights into the nuanced differences between the stem-ward taxa of each lineage. However, without molecular data constraining the topology, it is difficult to retrieve robustly-supported topologies and reconstruct ancestral nodes.

The present work synthesises these detached lines of inquiry, which are made less incongruous by the inclusion of numerous fossil taxa from the respective arctoid families and subfamilies. The addition of fossil taxa, and a broad sampling of extant taxa,

including both morphological and molecular data, allows for the reconstruction of ancestral nodes to be made from the phylogenetic method itself, rather than inferred from a surrogate or exemplary taxon.

Materials and Methods

Institutional Abbreviations

AMNH = American Museum of Natural History, New York, USA

BSP = Bayerische Staatssammlung für Paleontologie und Historische Geologie, Munich, Germany

CMN = Canadian Museum of Nature, Ottawa, Canada

FMNH = Field Museum of Natural History, Chicago USA

FSL = Departement des Sciences de la Terre, Universit. Claude Bernard, Lyon, France

JODA = John Day Fossil Beds, Kimberly, USA

LACM = Natural History Museum of Los Angeles County, Los Angeles, USA

MGL = Musée Geologique Cantonal, Lausanne, Switzerland

MNHN = Institut de Paleontologie, Museum National d'Histoire Naturelle, Paris, France

NMB = Naturhistorisches Museum Basel, Basel, Switzerland

NUFV = Nunavut Fossil Vertebrate Collection (housed in CMN)

ROM = Royal Ontario Museum, Ottawa, Canada

UOMNH = University of Oregon Museum of Natural History, Eugene, USA

USNM = Smithsonian Institution National Museum of Natural History

UWBM = University of Washington Burke Museum, Seattle, USA

YPM = Yale Peabody Museum, New Haven, USA

Selection of Taxa

Table 8 lists the taxa coded for use in the analyses, and identifies which taxa are included in each analysis. Completeness was considered when selecting fossil taxa. For example, *Eotaria*, the earliest-known otariid (Boessenecker and Churchill, 2015; Velez-Juarbe, 2017), was not included, as it is known only from mandibular and dental elements. A primary goal in the selection of fossil taxa was to sample early-diverging members of each lineage that do not depart significantly from the hypothetical ancestor at the base of Arctoidea. A representative taxon of every known family within Arctoidea, extinct or extant, is accounted for.

The earliest fossil odobenids and otariids are restricted to the North Pacific (Deméré et al., 2003). *Eotaria* represents the earliest-known stem otariid (Boessenecker and Churchill, 2015; Velez-Juarbe, 2017), but the taxon is very incompletely known, as are *Pithanotaria*, “*Thalassoleon*” *mcnallyae* and “*Thalassoleon*” *inouei*, taxa that likely represent early-diverging members of the *Callorhinus* (northern fur seal) offshoot (Deméré et al., 2003; Boessenecker and Churchill, 2015). “*Thalassoleon*” *mexicanus*, known from the late Miocene of the North Pacific, may be a stem otariid (Churchill and Boessenecker, 2014) or an early-diverging member of a clade containing all otariids excluding the aforementioned clade including *Callorhinus*. *Thalassoleon mexicanus* is well-represented by fossil remains, and is the earliest-known otariid included in the present analysis.

The fossil record of Odobenidae is much richer than that of Otariidae. Early-diverging odobenids, not departing significantly from the morphology of *Enaliarctos* and other stem pinnipeds, are well-known from Japan – *Prototaria* (Takeyama and Ozawa,

1984; Kohno, 1994; Kohno et al., 1995) – and Oregon, USA – *Proneotherium* (Kohno et al., 1995). Both *Prototaria* and *Proneotherium* are included in the present analysis, as are later-diverging fossil odobenids *Neotherium*, *Imagotaria*, and *Pontolis* (Kohno et al., 1995; Boessenecker and Churchill, 2013).

Until the late Pliocene, phocids were absent from the North Pacific, a piece of evidence which has previously been used to support pinniped diphyley (McLaren, 1960; Koretsky et al., 2016). Several phocids are known from the middle Miocene of eastern North America and the Paratethyan region (Koretsky, 2016). *Devinophoca* known from the early middle Miocene of Europe, displays a morphology transitional between *Enaliarctos* and later-diverging forms, notably retaining a carnassial notch on its P⁴ (Koretsky and Holec, 2002; Koretsky and Rahmat, 2014). *Devinophoca* is thus included in the present analysis.

Phocidae are further subdivided into two monophyletic groups: Monachinae and Phocinae. The fossil record of Monachinae is well-known, with fossil taxa displaying significant morphological diversity and geographical distributions. A pair of early-diverging fossil forms that are well-represented in the fossil record – *Acrophoca* and *Piscophoca* – are included in the present analysis. Phocinae is not as well-represented by completely-known fossil taxa, and so only extant phocines are included in the present analysis.

Desmatophocinae is an extinct clade that has typically been recovered within the pinniped crown group, either as sister to a clade of Phocamorpha (Berta and Wyss, 1994) or within the otarioid divergence (Mitchell, 1966; Repenning and Tedford, 1977; Boessenecker, 2016). Desmatophocines are represented in the present analysis by

Allodesmus and *Desmatophoca*.

Pinnarctidion has also previously been assigned to this group (Barnes, 1989; Berta, 1991; 1994; Berta and Wyss, 1994). However, a more detailed analysis of the traits aligning *Pinnarctidion* with desmatophocines showed *Pinnarctidion* lacks the synapomorphies of the group, and likely falls outside of crown Pinnipedia (Deméré and Berta, 2002). This result is not entirely surprising as *Pinnarctidion* retains a morphology similar to that of *Enaliarctos*, and specimens attributed to *Pinnarctidion* have even been misattributed to *Enaliarctos* in the past (Barnes, 1979). *Pinnarctidion* is included in the present analysis.

Enaliarctos is known from five species (*barnesi*, *emlongi*, *mealsi*, *mitchelli*, *tedfordi*) from the Pacific coast of North America (Berta, 1991). *Enaliarctos* lacks unambiguous characters in support of monophyly or paraphyly, and has thus been regarded as a meta-taxon (Gauthier, 1986; Berta, 1991). The different species of *Enaliarctos* are primarily distinguished based on dental differences, though there is some overlap between species with regards to these distinguishing dental traits (Cullen et al., 2014). Furthermore, *E. barnesi*, *E. tedfordi*, *E. emlongi*, and *Pinnarctidion rayi* display overlapping or adjacent stratigraphic distributions within the Yaquina Formation (Berta, 1991; Cullen et al., 2014). All five species of *Enaliarctos* were included in the analysis to explore the alpha taxonomy of this genus. Another later-diverging “enaliarctid”, *Pteronarctos*, is also included in the present study.

When pinniped diphyly was the prevailing paradigm, otariids and odobenids were believed to have diverged from a bear-like stock, likely represented by *Enaliarctos emlongi*. Meanwhile, *Potamotherium* was believed to be mustelidan ancestor to phocids

(McLaren, 1960; Tedford, 1976; de Muizon, 1982). Supporters of pinniped diphyly still identify *Potamotherium* as a link between terrestrial stem mustelids and phocids (Koretsky, 2014). Recognition of pinniped monophyly left *Potamotherium* in a precarious position. Wyss (1991) decoupled the intimate relationship between phocids and *Potamotherium* (to the exclusion of other pinnipeds) identifying *Potamotherium* as a mustelid offshoot that independently converged upon a similar ecology and morphology. In phylogenetic analyses, Wolsan (1993) and Kohno (1994) recovered *Potamotherium* as a stem pinniped. Baskin (1998) and Wang (2005) identified *Potamotherium* as an oligobunine, an early-diverging offshoot of Mustelidae. Finarelli (2008), in a full evidence phylogeny of Arctoidea, was unable to resolve the phylogenetic position of *Potamotherium*, recovering it in an incongruous position between the branches of *Mustela* and *Lutra*, while a morphology-only phylogeny recovered it as a sister taxon to phocids. Notably, both phylogenetic analyses of Finarelli (2008) identified a clade of oligobunines to the exclusion of *Potamotherium*.

The taxa typically referred to Oligobuninae include *Brachypsalis*, *Megalictis*, *Oligobunis*, *Promartes*, and *Zodiolestes* (Baskin, 1998; Wang et al., 2005; Finarelli, 2008; Valenciano et al., 2016). The oligobunines were ostensibly endemic to North America (Baskin, 1998). On the other hand, *Potamotherium* is known from thousands of specimens from Europe, but in North America is known only from mandibles, isolated teeth and scattered postcranial elements, that may actually belong to a different taxon (personal obs).

Oligobuninae is likely paraphyletic (Baskin, 1998). They may represent a monophyletic sister group (=paleomustelids) to neomustelids (Valenciano, 2016), a

gradient of stem mustelids approaching the crown group, or crown members distributed throughout Mustelidae (Finarelli, 2008). They are united by a mélange of ancestral (retention of carnassial notch and lack of a postlateral sulcus) and derived (reduction of postprotocrista and metaconule of P⁴, loss of alisphenoid canal, and reduction of M²/ M₂) features, but otherwise are highly variable with respect to a number of phylogenetically informative characters. For example, *Zodiolestes* has been cited as a stem procyonid (Wolsan, 1993), due to its deeply excavated suprameatal fossa (oft-cited as a procyonid feature, but also present in *Plesictis* and *Mustelictis*, which have been identified as stem mustelids (Schmidt-Kittler, 1981)) and lack of a posterior crest on the mastoid (Wang, 2005). *Megalictis* displays a lingually-located second molar, a feature thought to be diagnostic of pinnipedimorphs (Wolsan, 1993), though this feature is approached in the other oligobunines and *Mustelavus*, a small-bodied Oligocene arctoid that has been implicated in the origins of Oligobuninae (Sato et al., 2009). *Brachypsalis*, *Megalictis*, *Oligobunis*, *Promartes*, and *Zodiolestes* are included in the present analysis.

Mustelavus was frequently cited as a likely candidate to be the earliest-diverging mustelid known (Scott and Jepsen, 1936; Riggs, 1945; Baskin, 1998; Koepfli and Wayne, 1998), but has been more appropriately reinterpreted as prototypic of musteloid stock (Baskin and Tedford, 1996; Wang, 2005; Sato et al., 2009). Alternatively, *Mustelavus* has also speculated to be the progenitor of Semantoridae – a more inclusive group than Oligobuninae encompassing the typical North American taxa in addition to *Potamotherium*, and *Semantor* (Wolsan, 2005; Sato et al., 2009) – that has been identified as a sister group to the rest of Musteloidea.

Musteloidea encompasses four families: Mephitidae, Ailuridae, Procyonidae, and

Mustelidae. Identifying the earliest known representatives of each family is difficult, due to the rapid splitting events towards the base of this group (Doronina et al., 2015). The early-diverging members of each family display strikingly primitive morphologies (Radinsky, 1977; Wang et al., 2005). Their allocation to their respective crown groups can be founded on as little as a single phylogenetically informative character (Wolsan, 1993; Wolsan and Lange-Badré, 1996; Wang et al., 2005). Fossil taxa that may approximate the hypothetical condition at the base of musteloids include *Mustelavus* (Wang et al., 2005; Sato et al., 2012), and *Amphicticeps* (Schmidt-Kittler, 1991; Finarelli, 2008), both of which are included in the present analysis.

Molecular evidence suggests mephitids were the first of the extant lineages to split from the rest of the musteloids (Vrana et al., 1994; Ledje and Arnason, 1996b; Dragoo and Honeycutt, 1997; Flynn et al., 2000; Koepfli et al., 2008). Morphological analyses erroneously recover mephitids as late-diverging mustelids (Wang et al., 2005b; Finarelli et al., 2008), typically as sister to Lutrinae (Wozencraft, 1989b; Wyss and Flynn, 1993; Bryant et al., 1993; Baskin, 1998a; Wolsan, 1999). While it is difficult to reconcile the morphological evidence with the molecular, close inspection of mephitids reveals a retention of several features plesiomorphic to arctoids (Wang and Qiu, 2004) suggesting their similarities to mustelids are the result of convergence. Wang et al. (2005) further assert that the assignment of mephitids to Mustelidae relies on a priori assumptions about the hypothetical plesiomorphic condition at the base of Mephitidae-Lutrinae. Known fossil mephitids are all quite derived (Wang et al., 2005), but early diverging taxa include *Martinogale*, *Mydaus* (the extant Stink Badger), and *Promephitis*, the latter of which is included in the present study.

The phylogenetic position of Ailuridae befuddled systematists for over a century (Wang, 1997). *Ailurus* (red panda) was historically linked to *Ailuropoda* (giant panda), due to superficial similarities now considered to be caused by convergence. Later scholars noted similarities between *Ailurus* and Procyonidae, prompting the contention *Ailurus* was a member of the Procyonidae (Gregory, 1936; Simpson 1945; Hough, 1948; Schmidt-Kittler, 1981; Flynn et al., 1988; Wang, 1997; Baskin, 1998; Baskin, 2003; Ahrens, 2012), though some scholars still hypothesised of a closer relationship between *Ailurus* and Ursidae (Wyss and Flynn, 1993; Vrana et al., 1994). Recent molecular analyses have nearly unanimously recovered *Ailurus* as the sole extant member of its own family, branching off from the rest of musteloids (sans Mephitidae), shortly after the branching event of Mephitidae (Flynn and Nedbal, 1998; Flynn et al., 2000; Yu et al., 2004; Flynn et al., 2005; Sato et al., 2006; Sato et al., 2010) or before (Fulton and Strobeck, 2007).

The controversy over the phylogenetic relationships of Ailuridae with other arctoids also obstructed accurate identification of fossil ailurids (Wang, 1997). *Simocyon*, a puma-sized hypercarnivorous arctoid from the Middle Miocene to early Pliocene of Eurasia and North American, had been historically linked to early canids (Zittel, 1893; Matthew, 1924). However, comparison of *Simocyon* to possible fossil procyonids - *Broiliana*, *Amphictis* and *Alopecocyon* – elicited a reinterpretation of *Simocyon* as a procyonid (Beaumont, 1964, 1976, 1982, 1988) or as a stem arctoid (Wolsan, 1993). *Simocyon* has since been well-established to be an aberrant offshoot of a monophyletic ailurid family (Salesa et al., 2011). Several other fossil ailurids are well-known including the North American *Pristinailurus*, and the European *Amphictis*. *Amphictis* retains the

carnassial and basicranial morphology of early arctoids and caniformes (Baskin, 1998; Peigne et al., 2009), lacking the specializations toward an herbivorous diet observed in later ailurids (Salesa et al., 2011). *Ailurus*, *Amphictis* and *Simocyon* are included in the present analysis.

Like ailurids, procyonids have been suggested at times to be more closely related to ursids than to mustelids. However, the systematic position of procyonids within musteloids has been less volatile, with researchers consistently recovering procyonids as the sister group to mustelids (Wolsan, 1993; Flynn et al., 2005; Fulton and Strobeck, 2007; Finarelli, 2008; Sato et al. 2010; Ahrens, 2012). *Pseudobassaris* inhabited Europe 30-29 million years ago and was originally identified as a fossil procyonid (Pohle, 1917). Later researchers questioned this diagnosis and the distinction of *Pseudobassaris* as a new genus (Riggs, 1898; Hough, 1948; Schmidt-Kittler, 1981). Scholars have since upheld the generic distinction of *Pseudobassaris* (Baskin, 1998), but recovered it as a stem mustelid (Wang et al., 2005), stem musteloid (Wang et al., 2004) or outside the arctoid crown (Finarelli, 2008). Though it retains a morphology nearly identical to other stem mustelids, the suprameatal fossa of *Pseudobassaris* is decidedly procyonid-like (Wolsan and Lange-Badré, 1996). A dorsally deep suprameatal fossa is also found in specimens of *Plesictis* (Baskin, 1998; Paterson et al., In Prep), whose phylogenetic affinities are debated (Wang et al., 2004 Finarelli, 2008) and the oligobunine *Zodiolestes* (Baskin, 1998). Procyonids more closely resembling modern forms appear in the Early Miocene (Flynn et al., 1988; Baskin, 1998). *Broiliana* displays auditory and dental regions that confidently bespeak its procyonid affinities (Flynn et al., 1988; Wolsan, 1993), while *Angustictis* (Wolsan, 1993; Wolsan and Lange-Badré, 1996) and

Stromeriella (Flynn et al., 1988; Wang et al., 2005) have also been proposed as possible fossil procyonids. *Procyon*, *Broiliana*, *Stromeriella* and *Pseudobassaris* are all included in the present study.

The mustelid radiation is similarly cloudy, due to the volatile phylogenetic position of taxa towards the base of the group. *Plesiogale* and *Paragale*, a pair of European genera lacking a carnassial notch, appear to represent a morphology ostensibly characteristic of crown Mustelidae, and are thus the earliest taxa to be confidently placed within ‘Neomustelidae’ (Baskin, 1998). Both *Plesiogale* and *Paragale* are included in the present analysis, in addition to a variety of later-diverging mustelids (*Sthenictis*, *Taxidea*, *Neovison*, *Gulo*, *Lontra*, *Enhydra*).

The earliest-diverging ursids are the hemicyonines. While *Parictis* is frequently cited as an early diverging ursid, its affinities may lie with the possibly paraphyletic (Baskin, 2004; Wang et al., 2005) Amphicyodontinae, a group of late Oligocene and early Miocene ursid-like morphs that have been speculated to be the ancestors of pinnipeds (Tedford et al., 1994; McKenna and Bell, 1997; Rybczynski et al., 2009). *Phoberogale* (de Bonis, 2012), a Eurasian taxon first appearing in the late Eocene, is more easily accommodated into the Ursidae (Beaumont, 1965; de Bonis, 1973; Mitchell and Tedford, 1973; Ginsburg and Morales, 1998; Wang et al., 2005), and is included in the present analysis. Later-diverging ursids are represented by *Hemicyon*, *Arctodus*, and *Ursus* in the present analysis.

Kolponomos was originally identified as an aberrant twig of the procyonid lineage, but has since been identified as a member of Amphicyodontinae (Tedford et al., 1994; Wang, 2005; Rybczynski et al., 2009). Their bear-like appearance allows them to

ostensibly bridge the gap between earlier arctoids and the bear-like *Enaliarctos* (Tedford et al., 1994). The most completely known Amphicyodontids are *Pachycynodon* and *Amphicynodon* (Tedford, 1994), but the small-bodied *Parictis*, oft-cited as a stem ursid, has also been included (McKenna and Bell, 1997; Hunt, 1998). The semi-aquatic, wolf-sized *Allocyon*, known from only a single skull and associated right lower jaw from fluvial Oligocene deposits of the John Day Formation in Oregon, has also been allocated to this family (Tedford, 1994; Hunt, 1998). Hunt (1998) referred *Amphicticeps* to Amphicyodontinae, but its mélange of plesiomorphic features and peculiar derivations have addled systematists since its discovery (Matthew and Granger, 1924; Schmidt-Kittler, 1981). *Amphicticeps* was recovered in Amphicyodontinae by Wang et al. (2005), but this association was only weakly supported in a bootstrap analysis. Rybczynski et al. (2009) similarly recovered *Amphicticeps* in a clade of pinnipedimorphs sister to Amphicyodontinae. At the family level, Amphicyodontinae, if monophyletic, could alternatively serve as the sister group to Mustelida (pinnipeds + musteloids) or Arctoidea (pinnipeds + musteloids + ursids). *Kolponomos* and *Allocyon* are both included in the present study.

Canidae was identified as an ideal outgroup for this analysis, reflecting the close phylogenetic relationships between canids and arctoids, and the availability of molecular data for the group. The earliest diverging canids are *Prohesperocyon* and *Hesperocyon*. The latter is well-represented in the fossil record, and does not display the specializations observed in later-diverging canids, so it is included in the present study. *Canis* is included as the lone extant canid.

The extinct Amphicyonidae are represented in our analysis by *Temnocyon*. Amphicyonidae have conventionally been placed within the arctoids (Wolsan, 1993; Wyss and Flynn, 1999) though their precise placement within Arctoidea has been volatile. It should be noted Amphicyonidae likely actually falls outside crown Caniformia (Wesley-Hunt and Flynn, 2005; Tomiya and Tseng, 2016), though our analysis is not comprehensive enough to test such a hypothesis. In the present study, *Temnocyon* is included as an in-group unit in all but one of our analyses, an inclusion that may appear ill-considered in the future, but is necessary for testing conventional hypotheses of caniforme relationships.

Analysis of Molecular Data

Following Sato et al. (2009), nucleotide sequences of five nuclear coding genes were obtained – APOB (Apolipoprotein B), BRCA1 (Breast cancer 1, early onset), RAG1 (Recombination activating gene 1), IRBP (Interstitial retinol binding protein 3), VWF (Von Willebrand factor) – for a selection of extant arctoids (Table 9). The sequence data were downloaded from GenBank (NCBI, and accession numbers are listed in Table 9). Sequences were aligned using the MUSCLE alignment in Mesquite (Maddison and Maddison, 2015) and trimmed manually for identical lengths. Each aligned gene was allocated to a discrete partition within the dataset. To determine the evolutionary models of best fit for each data partition of molecular data, marginal likelihoods for each available model were calculated and compared separately for each partition using the stepping stone method (Xie et al., 2010), a path sampling method which obviates the controversial use of the harmonic mean method to estimate likelihood (Fan et al., 2010).

Table 10 lists the models and variants that were considered, and their marginal likelihood scores when subject to a Markov Chain Monte Carlo analysis of 5,500,000 generations and 50 steps. The models with the highest average marginal likelihood score, (averaged between the two runs), were selected. The GTR + gamma model was selected for VWF, APOB, and BRCA1, and the GTR + invgamma model was selected for RAG1 and IRBP. The models-of-best-fit were later applied to their relevant data partitions in the Bayesian analyses.

At least one taxon from each extant caniform family was included in the molecular analysis – Canidae (*Canis lupus*), Ursidae (*Ursus arctos*), Mephitidae (*Mephitis mephitis*), Ailuridae (*Ailurus fulgens*), Procyonidae (*Procyon lotor*), Mustelidae (*Gulo gulo*, *Lontra canadensis*, *Enhydra lutris*, *Neovison vison*, *Taxidea taxus*), Odobenidae (*Odobenus*), Phocidae (*Cystophora cristata*, *Erignathus barbatus*, *Halichoerus grypus*, *Phoca vitulina*) and Otariidae (*Callorhinus ursinus*, *Eumetopias jubatus*, *Zalophus californianus*). The inclusion of taxa was based on the availability of their selected genes on genbank. Gaps and missing characters were treated as missing data. *Canis lupus* was specified as the outgroup.

The analyses reported herein were initially run in MrBayes v3.2.6 (Huelsenbeck, 2001) for 5,000,000 generations, with a sampling frequency of 1000 and a diagnostic frequency of 1000. To ensure convergence upon similar results, two runs were requested for the analysis. Stationarity and convergence of the posterior probabilities were gauged using Tracer v1.6 (Rambaut, 2007) for OSX. Convergence of parameters was identified when the plot of the log likelihoods (“the Trace line”) varied about a constant value. After accepting convergence, runs considered sufficiently long when the effective sample sizes

(ESS's) for each trace rose above 200. AWTY (Wilgenbusch et al., 2004) was offline as of this analysis, so no test of convergence of tree topologies was used. Inspection of the trace plots also allowed us to identify the burn-in of each analysis, which was subsequently discarded. Following termination of the runs and discarding of the burn-in, the consensus tree showing all compatible clades was requested (contype=allcompat).

Analysis of Morphological Data

In molecular phylogenetics, sources of systematic error are those which may cause an analysis to fail to accurately model evolutionary processes (Phillips et al., 2004). Systematic errors in molecular phylogenetics have been thoroughly investigated (Simmons and Freudenstein, 2003; Gruber et al., 2007; Li et al., 2008; Liu et al., 2010). In morphological phylogenetics, possible systematic errors are not well-understood, and their potential to mislead phylogenetic topologies has not been well-explored (Dávalos et al., 2014). Encouragingly, recent experimental work by Zou and Zhang (2016) suggests morphological characters can provide nearly as much phylogenetic utility as molecular characters if appropriately generated. Morphological characters are thought to be more susceptible to convergence than are molecular characters (Givnish and Sytsma, 1997) but this may be caused by the difficulty in devising characters that accurately model phenotypic evolution.

Additionally, the use of non-independent characters remains one of the most pernicious aspects of phylogenetic analyses based on morphological characters (Zou and Zhang, 2016). To combat the non-independence of characters, Zou and Zhang (2016) suggest utilising fewer characters, and preferentially selecting characters with multiple

states (but see Brazeau, 2008 for a view on common misapplications of multi-state characters). This approach was followed in the present study.

Eighty-two craniomandibular characters, fifty dental characters, and seventy-two postcranial characters were coded when possible for all taxa in the analysis. While some characters are novel, the majority of characters were derived from previous phylogenetic analyses of Carnivora, including those focussing on pinnipeds (Berta and Wyss, 1994; Kohno, 1996,2006; Deméré and Berta, 2001, 2002, 2005; Boessenecker and Churchill 2013,2015; Amson and Muizon, 2014; Churchill and Boessenecker, 2014; Furbish, 2015) musteloids (Bryant et al., 1993; Wolsan, 1993; Ahrens, 2013; Valenciano et al., 2016), arctoids (Wang, 2005; Tedford, 1994; Finarelli, 2008), and carnivorans more broadly (Wyss and Flynn, 1993; Wesley-Hunt and Flynn, 2005; Spaulding and Flynn, 2011; Tomiya and Tseng, 2016) (see Appendix C for full character list). Many of these characters were then modified, either by editing existing character states or by adding character states, to better reflect the diversity of these characters across arctoids. All changes are noted in Appendix C. All taxa were specifically coded for this study.

Recent phylogenetic analyses of pinnipeds (Deméré and Berta 2002; Deméré and Berta, 2003) have attempted to quantify and discretize characters that gauge nuanced differences in size and/or shape of morphological features, an approach followed in the present analysis. Further work on the morphological characters used in the study of fossil carnivorans should use statistical techniques to test the discretization or “binning” of different character states (Prieto-Márquez, 2010).

A representative from every known arctoid family was coded, including members of the extinct Amphicyonidae, Oligobuninae and Desmatophocidae. When possible, adult

male specimens were selected for character coding, due to the high sexual dimorphism displayed in many modern (Gittleman and Van Valkenburgh, 1997) and fossil arctoids (Hunt, 2002; Cullen et al., 2014).

To code their character states, specimens representing the fossil taxa were observed in person. Data for certain characters were also gathered from the literature if not discernible in the specimens available to us (Table 11). Those concerning the internal cranial anatomy were inferred from video files of CT scans spanning the different axes of the cranium (from www.digimorph.org) and the literature (Ahrens, 2012; Grohé et al., 2016; Geraads and Spassov, 2016).

The Mk model is the default model for Bayesian inference of morphological data, and was employed in all Bayesian analyses of morphological data. The stepping-stone method was used to explore the fit of the rates (equal, gamma, invgamma) to the Total Morphology partition. The stepping-stone analysis was run for 1,100,000 generations and used 50 steps. The gamma rates model had the highest marginal likelihood score, and was thus selected for all morphological partitions subject to Bayesian inference. Besides model selection, the other parameters of the Bayesian Inference analyses of morphological data followed those previously outlined for the analyses of molecular data.

Among paleontologists, parsimony has been the preferred method of phylogenetic inference of morphological datasets, likely owing to its greater precision (O'Reilly et al., 2016) and computational simplicity. However, Bayesian inference has been shown to be a more accurate estimator of phylogeny than parsimony, even with morphological datasets (Wright and Hillis, 2014; O'Reilly et al., 2016). In the present study, greater

attention is paid to the Bayesian Inference analyses. Parsimony-based methods were primarily employed to allow for a more nuanced inspection of character evolution.

PAUP software v4.0b10 (Swofford, 2002) was used to run the parsimony analyses. Heuristic searches were performed for the following data sets: Total Morphology and Craniomandibular + Dental Only. The searches were repeated with a backbone constraint, identified from the Bayesian analysis of molecular data, enforcing the following topology:

(Canis(Ursus(((Erignathus(Eumetopias, Odobenus))(Mephitis(Ailurus(Procyon(Taxidea(Gulo(Neovison(Enhydra, Lontra)))))))))))). For each analysis, *Canis* and *Hesperocyon* were defined as the outgroup taxa. Analyses of the Total Morphology dataset employed the TBR algorithm, 100 random addition sequence, and requested 10,000 max trees. Analyses of the craniomandibular dataset also employed the TBR algorithm, but used 10 random addition sequences, and requested 100,000 max trees, with 10,000 max trees set as the limit for each random addition sequence. Bremer Decay Indices (Bremer, 1988), calculated manually in PAUP, were used to assess the strength of support for internal nodes. The 50% majority-rule consensus trees for each analysis are reported. Characters were optimized onto a tree with the same topology as the 50% majority-rule consensus tree (excepting the sole polytomy at the base of Mustelidae + Procyonidae), from the Total Morphology analysis, using the DELTRAN algorithm. Apomorphies were obtained for the two primary nodes of interest, and then optimized using the ACCTRAN algorithm. Unambiguous synapomorphies were identified as those characters that appeared at the same node using both modes of optimization.

Total Evidence Analysis

The total evidence analysis (combined analysis of morphological and molecular data) was carried out on a selection of 67 caniform taxa. Bayesian inference was performed in MrBayes v3.2.6 (Huelsenbeck, 2001). Data was partitioned into 6 sets – Morphological, APOB, BRCA1, RAG1, IRBP, VWF. The Mk model was applied to the Morphological partition. The molecular models were the same ones selected for the Molecular Only analysis. Rates of character evolution were assumed to vary across sites and were assigned a gamma distribution. To allow each partition to vary according to its own set of parameters, all parameters were unlinked. The rate prior was set to variable for all partitions (prset ratepr=variable), to allow for different rates of evolution across partitions. *Canis lupus* was specified as the outgroup.

Results

While the foremost aim of the analysis is to reconstruct the pinniped branch of the caniforme family tree using a total evidence analysis, reported herein are also phylogenetic trees recovered from the following partitioned datasets: molecular only, all morphological, craniomandibular only, craniomandibular + dental only, and postcranial only.

Molecular Only

The molecular only topology (Figure 2.4) recovers a monophyletic Pinnipedia, with otariids and *Odobenus* sharing a more intimate relationship. Musteloids are identified as the sister group of pinnipeds. Mephitids are the first family to diverge from

the rest of the musteloid stock, followed by ailurids. Procyonids and mustelids are recovered as sister lineages, with *Taxidea* diverging toward the base of mustelids. All relationships are very strongly supported (pp=1.00).

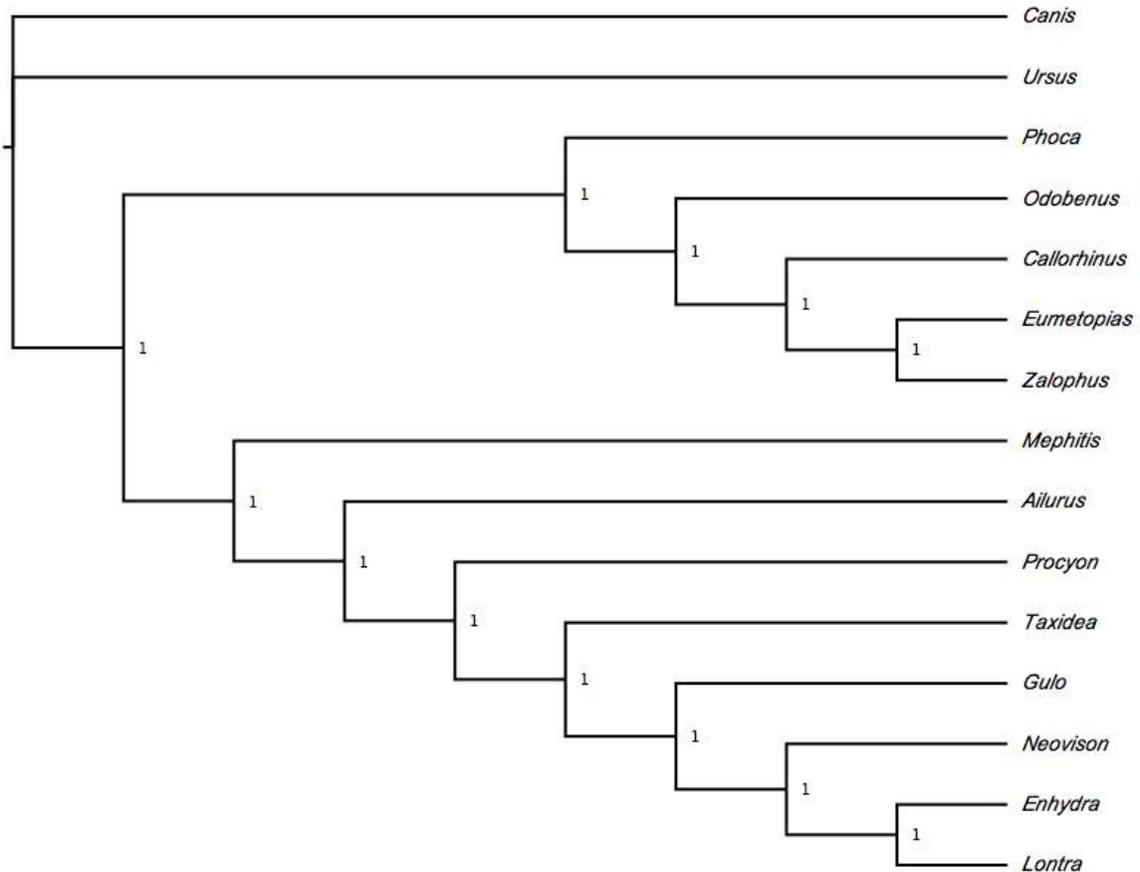


Figure 2.4. Majority-rule consensus tree of molecular-only partition using Bayesian Inference.

Numbers at nodes are posterior probability values.

Morphology only

Total Morphology A crown group Pinnipedia, including odobenids, otariids, phocids, and desmatophocids is recovered with moderate support (pp=0.54) in the Total Morphology analysis (Figure 2.5). Within this crown group, an unconventional coupling

of otariids and phocids is recovered. This aberrant otariid-phocid pairing is reasonably well-supported (pp=0.72). Desmatophocids are recovered as sister to this group (pp=0.72). Monachines are not recovered as monophyletic, but along the sequence leading to a well-supported monophyletic Phocinae (pp=1.00). *Amphicticeps* is recovered as the earliest diverging member of the pinniped lineage (pp=0.49) and the musteloids are recovered as the sister group to pinnipeds (pp=0.13).

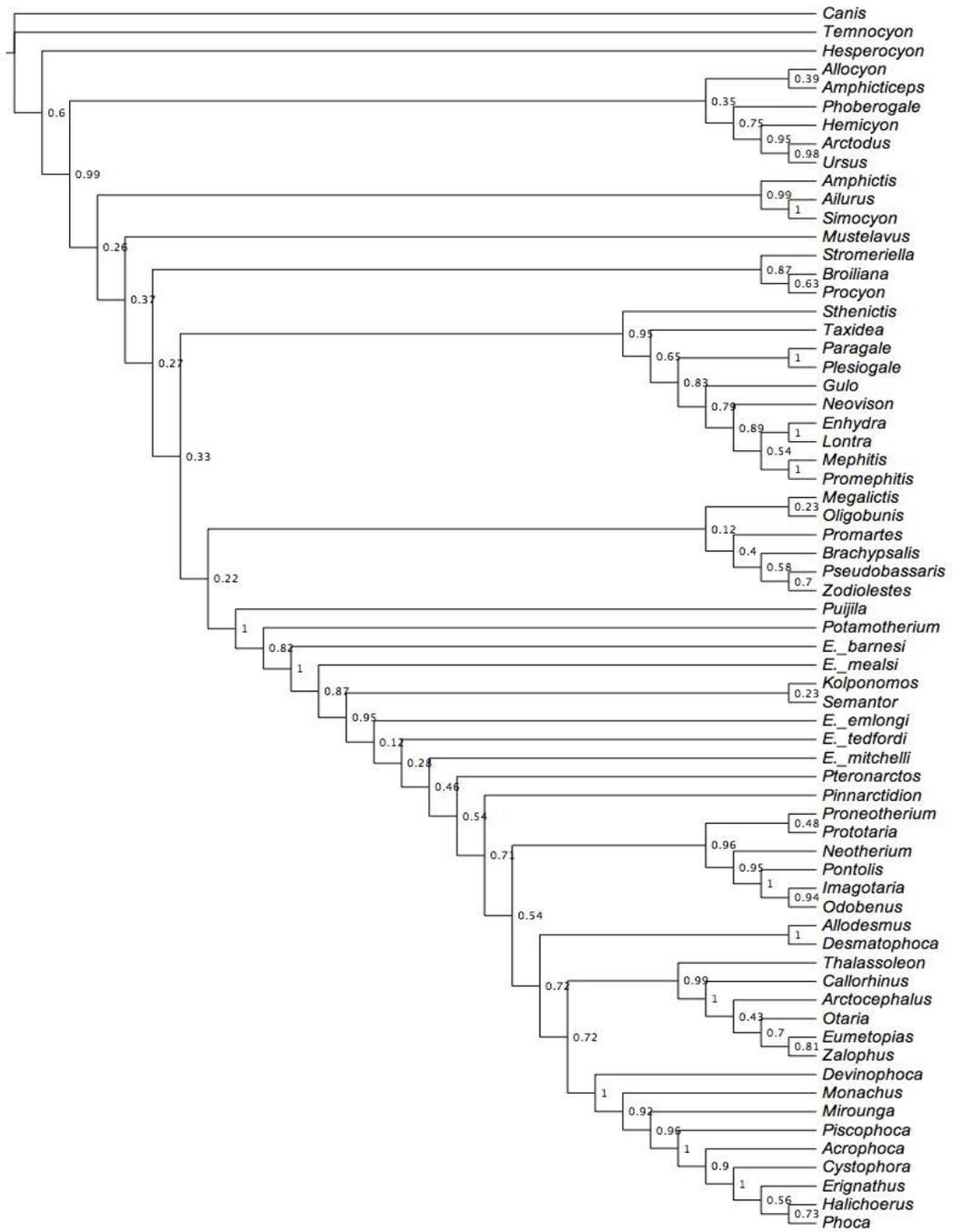


Figure 2.5. Majority rule consensus tree of Total Morphology partition from Bayesian Inference Analysis. Numbers at nodes are posterior probability values.

Craniomandibular Only The present craniomandibular-only Bayesian Inference analysis (Appendix A: Figure A.1) recovers a Phocomorpha group (Berta and Wyss, 1994), with the phocid stem occupied by a sequence through *E. mitchelli*, *Pinnarctidion*, *Allodesmus* and *Desmatophoca*, prior to the origin of *Devinophoca* and the true phocids. The monachines are suggested to be paraphyletic. *Pteronarctos* is identified as the earliest-diverging odobenid (pp=0.51). The sister group of pinnipeds is identified as an inclusive Ursidae similar to that recovered by Wyss and Flynn (1993), including *Ursus*, *Arctodus*, *Ailurus*, *Amphictis*, *Simocyon*, *Amphicticeps*, *Allocyon*, *Phoberogale*, and *Mustelavus*, though this node is very weakly supported (pp=0.21). *Kolponomos* is not recovered within this ‘Ursidae’, but is again recovered along the pinniped stem. Within this same cranial-only Bayesian analysis, the musteloids are suggested to be paraphyletic, as the mephitid divergence is placed well before the independent branching events of the Procyonidae and the Mustelidae.

Craniomandibular + Dental Phocids and desmatophocids are identified as sister groups (pp=0.52) in the analysis of the craniomandibular + dental dataset (Appendix A: Figure A.2). Monachinae is not identified as monophyletic. *Devinophoca* is recovered as the earliest-diverging phocid (pp=0.90). A strongly-supported Neomustelidae + Mephitidae clade (pp=0.93) is recovered as the sister group to a weakly-supported Procyonidae + Oligobuninae clade (pp=0.14). This combined clade serves as the sister to pinnipeds (pp=0.47).

Postcranial Only The postcranial only analysis recovers a similar topology to the other morphological partitions (Appendix A: Figure A.3). A crown group Pinnipedia, with a closer grouping of otariids and phocids, is again recovered. *Allodesmus* and *Desmatophoca* are recovered within Otariidae (pp=0.44), identified as diverging after *Thalassoleon*. *Devinophoca* is recovered as an early-diverging phocine (pp=0.84), as is *Piscophoca*, though the latter is only weakly supported (pp=0.41). The pinniped stem comprises, in order of divergence, *Puijila*, *Potamotherium*, *E. mealsi* and *Semantor*. The sister group is identified as a very weakly-supported Procyonidae + Mustelidae group (pp=0.13), anomalously including *Simocyon*, as a procyonid (pp=0.27) and *Phoberogale*, as sister to this *Simocyon-Procyon* pairing (pp=0.17). *Mephitis*, *Ailurus*, and *Ursus* are identified as diverging prior to this split.

Parsimony analysis of morphology only The parsimony analysis of the Total Morphology data set, without constraints, recovered 48 most parsimonious trees with 1036 steps. A strict consensus tree (Figure 2.6) identifies otariids and odobenids as sister groups within a monophyletic Pinnipedia. Desmatophocines, excluding *Pinnarctidion*, are recovered within Otarioidea, though their divergence predates the otariid/odobenid split. A procyonid-mustelid clade is recovered as the sister group to the pinnipedimorphs, to the exclusion of ailurids. As in the Bayesian analysis of morphological data, the Mephitidae are recovered as sister to Lutrinae. While the tree, in general, is moderately well-resolved (consistency fork index (CFI)=0.797), the base of pinnipeds is not well-resolved, recovering a polytomy of phocids, otarioids, odobenids and desmatophocids.

The 50% majority-rule tree (Appendix A: Figure A.4), provides some further resolution (CFI=0.875).

Strict consensus tree

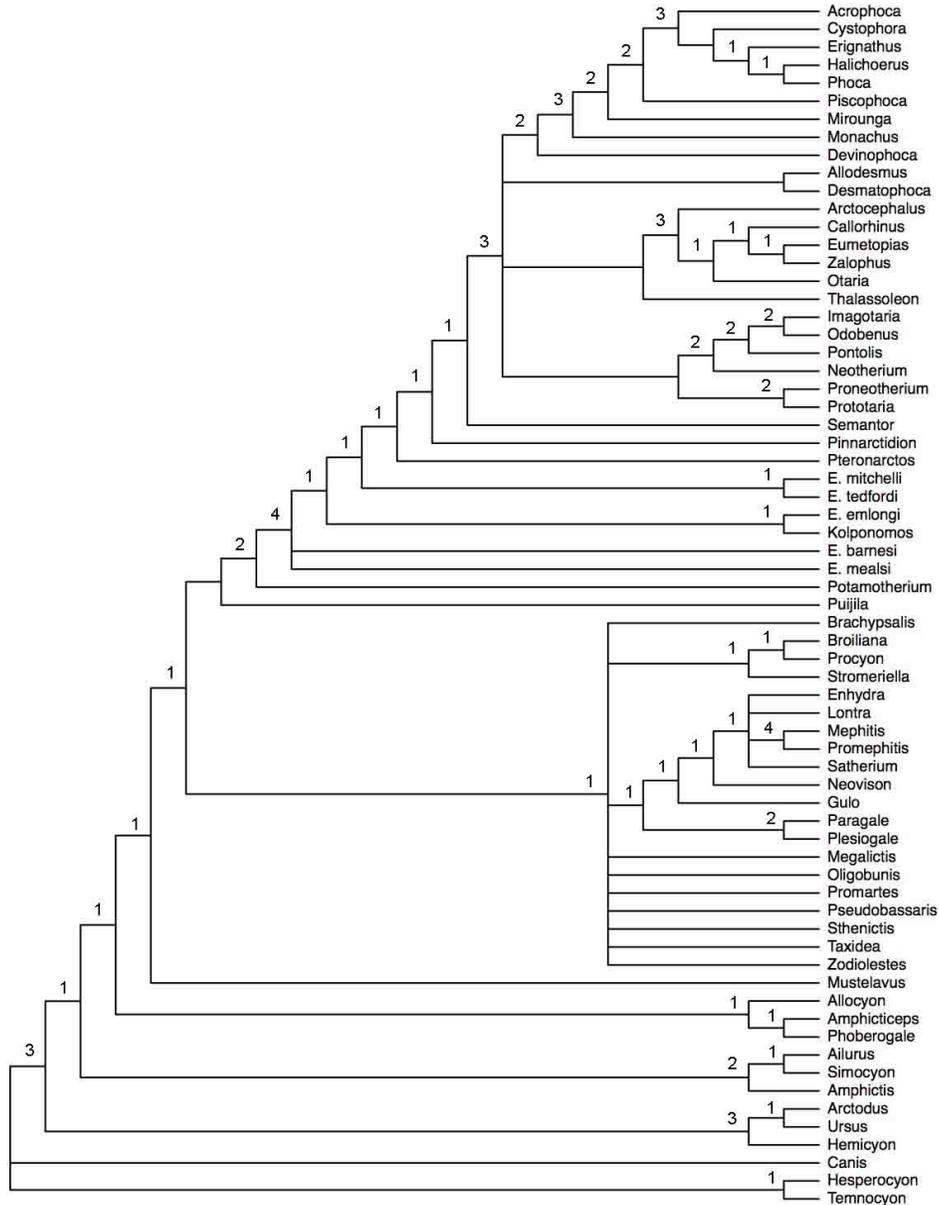


Figure 2.6. Strict consensus tree from heuristic search of Total Morphology dataset without a molecular backbone constraint. Numbers below nodes indicate Bremer Decay Indices for that node. Indices above five are not reported.

With a backbone constraint of relationships inferred from the molecular analysis, an additional 14 steps are required to produce the most parsimonious trees. In the strict consensus tree (Figure 2.7; CFI=0.791), a similar Pinnipedimorpha clade is recovered. Mephitids and ailurids return to their probable position within Musteloidea. The topology does not change significantly in the 50% majority-rule tree (Appendix A: Figure A.5).

Analysis of the craniomandibular data, in isolation, results in some key topological differences. Thirty thousand most parsimonious trees were recovered, with 820 steps. Again, the strict and semistrict consensus trees are poorly resolved compared to the 50% majority rule tree (CFI=0.938) (Appendix A: Figure A.6) As in the Bayesian Inference analysis of the same data-set, desmatophocids (including *Pinnarctidion*) are recovered along the phocid stem. This phocoid group recovered in a polytomy with odobenids (together representing the Phocamorpha of Berta and Wyss, (1994)) and *Semantor*. *Amphicticeps* is identified as the earliest-diverging member of the pinniped lineage. When the molecular backbone is enforced, and the 50% majority rule tree (Appendix A: Figure A.7; CFI=0.891) is requested, desmatophocids remain on the phocid stem, and *Allocyon* and *Phoberogale* migrate to the pinniped stem as the earliest diverging members of this lineage, followed by *Amphicticeps*.

Total Evidence Analysis

The results of the total evidence analysis (TEA) are displayed in Figure 2.8. Three total evidence analyses were run. The first is inclusive of all taxa. The second and third exclude *Puijila*, and *Potamotherium*, respectively. Many of the relationships are not strongly supported by posterior probability values.

Strict consensus tree

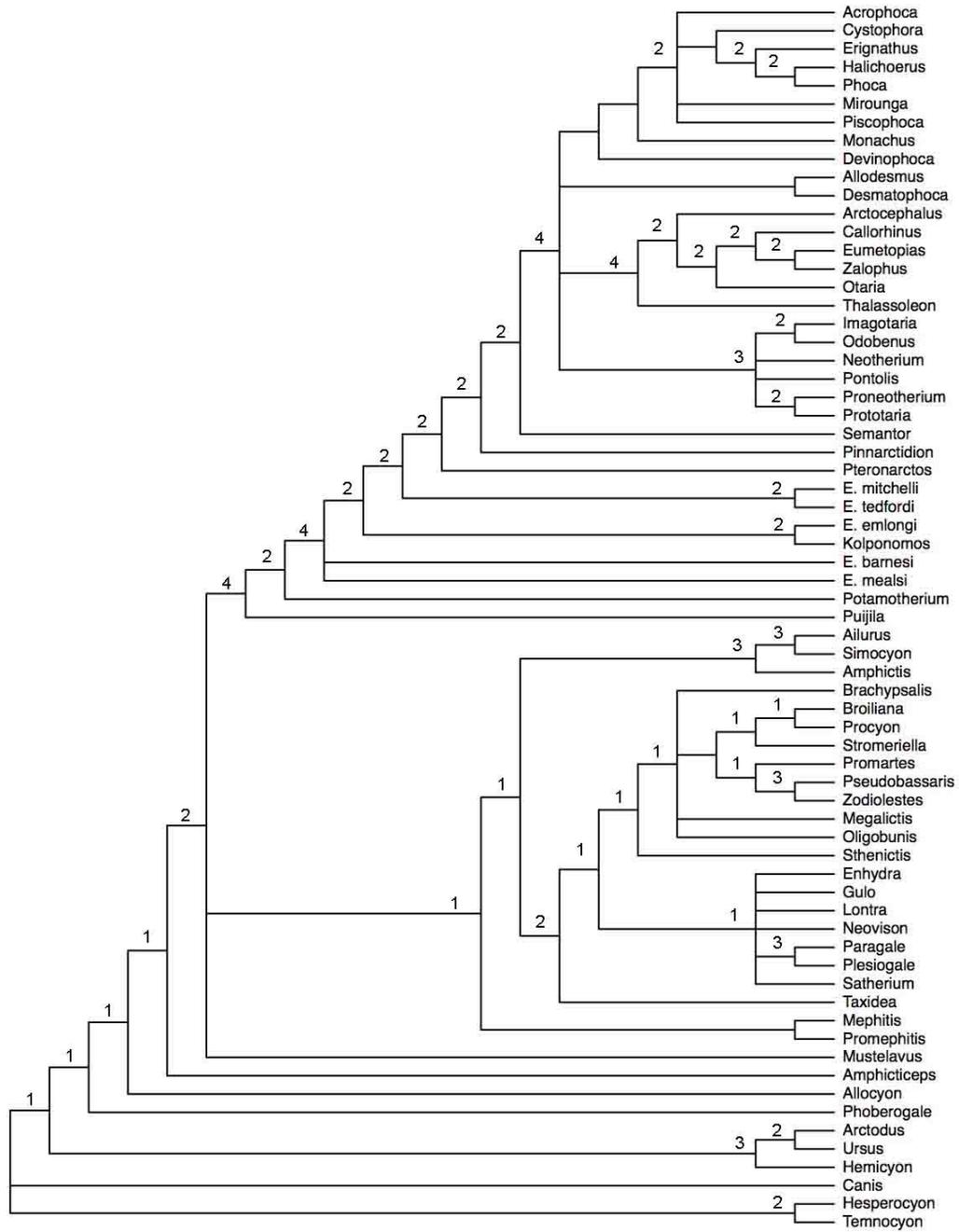


Figure 2.7. Strict consensus tree from heuristic search of Total Morphology dataset with a molecular backbone constraint. Numbers below nodes indicate Bremer Decay Indices for that node. Indices above five are not reported.

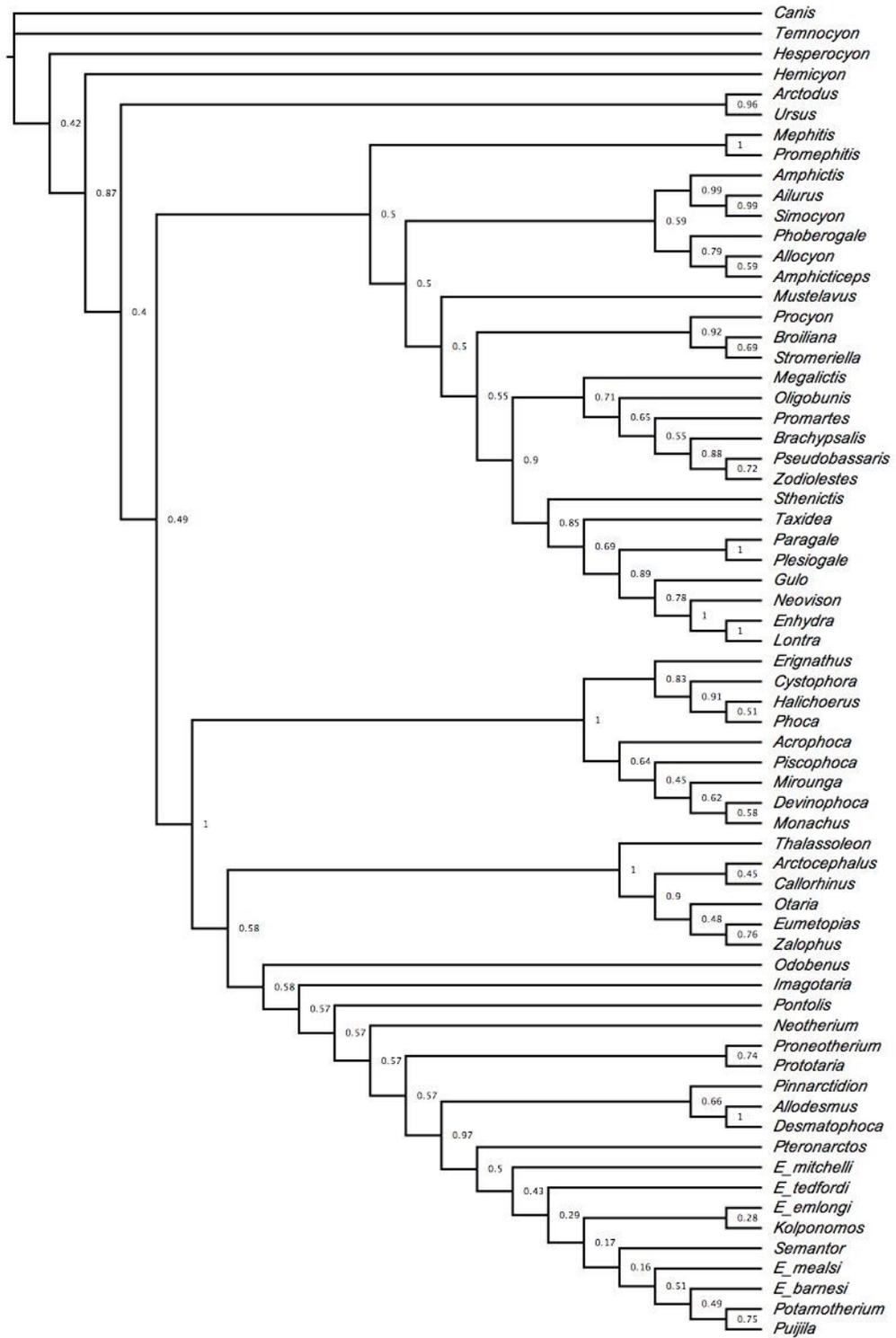


Figure 2.8. Majority rule consensus tree of total evidence analysis. Numbers at nodes are posterior probability values.

The TEA recovers a topology in agreement with molecular analyses on the relationships between extant families. Otariidae and Odobenidae are recovered as sister groups, rounded out by Phocidae in a monophyletic Pinnipedia. Musteloids are identified as the sister group to pinnipeds.

Many of the other relationships are not strongly supported by posterior probability values. Within the odobenines, a clade of early-diverging pinnipedimorphs is recovered. Within the clade are the desmatophocines and enaliarctines, along with *Puijila*, *Potamotherium*, *Semantor*, and *Kolponomos*. *Enaliarctos* is recovered as paraphyletic, as the different species are distributed in a clade also containing *Kolponomos*. Besides a strong coupling of *Potamotherium* and *Puijila* (pp=0.75), all of these relationships are very poorly supported (pp<0.51).

Monophyly of the desmatophocines (*Pinnarctidion*, *Desmatophoca*, *Allodesmus*) is well-supported in the total evidence analysis (pp=0.66), and a closer association between *Allodesmus* and *Desmatophoca* is strongly supported.

Discussion of Phylogenetic Analyses

Molecular data only by Bayesian Inference

The topology of the molecular-only partition resembles that of other phylogenetic analyses of molecular datasets (Flynn et al., 2005; Arnason, 2006; Fulton and Strobeck, 2007; Sato et al., 2010). This is unsurprising, though still noteworthy, as the inclusion of additional otariid and phocid taxa did nothing to disrupt the inter-familial relationships identified or their level of support from posterior probability values. The strong posterior

probability values suggest the relationships identified in the molecular-only analysis can also be confidently used to construct a backbone for the later parsimony analyses.

Morphology data only by Bayesian Inference

Total Morphology

The topologies of the five morphological partitions are highly incongruent with respect to one another, though all analyses recover a monophyletic Pinnipedia. Without a molecular backbone constraint, most previously published morphological phylogenetic analyses (excepting Kohno, 1993) recover Ursidae as the sister to pinnipeds (Berta and Wyss, 1994; Tedford et al., 1994; Furbish, 2015). In contrast, the Total Morphology partition in the present study recovered musteloids as sister to pinnipeds, which is consistent with analyses of molecular data (Flynn et al., 2005; Arnason, 2006; Fulton and Strobeck, 2007; Sato et al., 2010). However, the relationships within Musteloidea, found in the Total Morphology partition, are not in total agreement with the molecular analysis, as mephitids are recovered within the mustelid radiation and ailurids are excluded from the group entirely.

Unexpectedly, the total morphology partition also recovered otarioids and phocids as sister taxa. To our knowledge, otariids and phocids have not previously been recovered as sister groups, to the exclusion of odobenids, in any published phylogenetic analysis, though an early divergence of odobenids was suggested by Lento et al. (1995). In the present analysis, this unconventional relationship is presumably caused by a lack of transitional phocids and otariids. *Prototaria*, the earliest-diverging odobenid in the analysis, is a conspicuous link between the hypothetical last common ancestor of

pinnipeds and later-diverging odobenids (Kohn, 1994). On the other hand, *Devinophoca* and *Thalassoleon*, the earliest-diverging phocid and otariid, respectively, in the analysis, share many features with one another, that presumably arose in parallel as the two lineages became more aquatically specialized. Many of these shared features are absent in *Prototaria*, and *Proneotherium*, another early-diverging odobenid, but appear in later-diverging odobenids like *Imagotaria*.

Pinnarctidion has found to be removed from Desmatophocidae to a position outside of the pinniped crown group. *Desmatophoca* and *Allodesmus* are highly derived, displaying several proposed pinniped synapomorphies (Berta and Wyss, 1994) and appear well-removed from pinnipedimorphs. However, *Pinnarctidion* retains many features otherwise thought to characterize stem pinnipeds. These include: retention of an intrabullar pseudoseptum; presence of pseudosylvian sulcus; presence of fossa muscularis; presence of protocone shelf on P³; retention of fovea for ligamentum teres femoris; unreduced trochanteric fossa; presence of nasolabialis fossa; small antorbital process; large inferior petrosal sinus.

The most notable transgression in the Total Morphology analysis is the outdated placement of mephitids (*Mephitis* + *Promephitis*) as sister to the lutrine group. While morphological phylogenies consistently identify skunks as mustelids (excepting the phenetic inferences of Radinsky et al., 1977), molecular evidence overwhelmingly favors a branching event of Mephitidae towards the base of Musteloidea (Dragoo and Honeycutt, 1997; Flynn et al., 2005; Sato et al., 2010). In spite of their mustelid-like morphology, extant mephitids display a mosaic of ancestral/primitive (retention of postprotocrista of M₁, short palate) and uniquely-derived (reduction of osseus tentorium,

presence of mastoid sinus, absence of entepicondylar foramen of the humerus, reduction of baculum) features that reveal their independent derivation from the musteloid stock.

Craniomandibular

Cranial characters have been generously sampled in pinniped phylogenies. Among modules, the basicranial region has been particularly well-sampled in such studies. The phylogenetic utility of this region in Carnivora has been implied since the work of Turner (1848) and Flower (1869). Notably, greater scrutiny of the inner ear and middle ear prompted Wyss (1987) to present an early and compelling argument for pinniped monophyly. Investigation of the basicranial region has also provided valuable insights into the evolution of other caniforme groups (Hough, 1948; King, 1966; Hunt, 1974; Radinsky, 1977; Schmidt-Kittler, 1981; Hunt and Barnes, 1994). Accordingly, the tacit significance ascribed to the basicranium has been confirmed by recent studies demonstrating the basicranial region tends to manifest a strong phylogenetic signal in carnivorans (Goswami and Polly, 2010), and tetrapods more broadly (Liebermann et al., 2000; Cardini and Elton, 2008; Maddin, 2011). The basicranium develops early in ontogeny, and ossifies mostly from a cartilaginous precursor (Liebermann et al., 1996). As such, it is ostensibly less susceptible to non-genetic factors and thus less reflective of ecological adaptation (Liebermann et al., 1996; Cardini and Elton, 2008). Recently, high resolution micro-computed tomography has allowed for a more detailed inspection of the basicranial region, particularly those areas which are inaccessible without some level of specimen destruction.

The craniomandibular-only partition, as analysed in MrBayes, recovers many relationships that were previously supported by morphological evidence (e.g. Ursida, Phocamorpha) (Wyss, 1987; Berta and Wyss, 1994; Tedford et al., 1994; Hunt, 1994), but have been since discredited by molecular analyses (Flynn et al., 2005; Arnason et al., 2006; Fulton and Strobeck, 2007; Sato et al., 2010). This is likely reflective of the high dependence of cranial characters in phylogenetic analyses of pinnipeds, excepting Berta and Wyss (1994). Nevertheless, the well-supported inclusion of *Potamotherium*, *Puijila*, and *Kolponomos* within the pinnipedimorph clade strongly suggests that is where their phylogenetic affinities lie.

Craniomandibular + Dental

Dental characters are sparsely used in pinniped phylogenies, typically representing only a small portion of the morphological characters. This is understandable, given the homodont dentition observed in extant pinnipeds. However, as the purpose of this study is to infer the relationships of pinnipeds to terrestrial carnivorans, a broader sample of dental characters was employed. Characters related to mastication are thought to be more susceptible to homoplasy in mammals (Wood, 1988; Skelton and McHenry, 1992; Begun, 1994; Collard and Wood, 2001; Sansom et al., 2016). Liebermann et al. (1996) suggested the masticatory system of hominids is more homoplastic because of its derivation from intramembranous bone, which, in development, is more sensitive to mechanical force, and other ecological and functional factors. Furthermore, characters related to cusp and root morphology may be unusually susceptible to avatism in certain lineages (Kear et al., 2016). For example, Drehmer et al. (2004) identified the occurrence

of extramandibular teeth in nearly ten percent of a sample of specimens representing the southern sea lion (*Otaria*), a troubling discovery as many fossil taxa included in phylogenetic analyses are known only from a single specimen (the present study notwithstanding).

The addition of dental characters to the craniomandibular dataset does not significantly impact the topology of the pinniped branch of the tree. However, the sister group shifts from a lightly-defined “Ursidae” to a Mustelidae + Procyonidae + Mephitidae clade, though this node is not strongly supported (pp=0.47).

Postcranial

As with dental characters, postcranial characters are occasionally omitted from phylogenies assessing the inter-relationships of arctoids. Pinnipeds are often excluded from phylogenetic (Spaulding and Flynn, 2011) and non-phylogenetic (Samuels et al., 2013) studies of arctoids. The extreme modifications associated with aquatic adaptations are believed to obscure the phylogenetic and ecological signals of postcrania, occasionally provoking an a priori assumption that postcranial characters may be pernicious to such analyses. The lack of postcranial material that may be reliably attributed to fossil taxa has also dissuaded many researchers from including postcranial characters in their phylogenetic analyses, under the assumption a substantial amount of missing data may be inimical to the accuracy of a phylogenetic analysis. While there is evidence such a phenomenon exists (Sansom, 2014; Pattinson et al., 2015), other analyses have found that including taxa with missing data can improve an analysis’ capacity to recover an accurate topology (Wiens, 2003; 2006). More experimental studies are likely

required to solve this issue. To mitigate its potential effects, we report trees recovered from various partitions of the collected data (Mounce et al., 2013; Pattinson et al., 2015).

Berta and Wyss (1994) included a high proportion of postcranial characters in a comprehensive phylogenetic analysis of pinnipeds. Herein, several new characters, many of which relate to the highly variable calcaneostragalar complex (Polly, 2008), were introduced (see Appendix C).

The topology recovered from the analysis of the Postcranial Only partition does not depart significantly from the other partitions with regards to inter-familial relationships, but some fossil taxa are recovered in peculiar positions (e.g., *Phoberogale*, *Simocyon*, *Megalictis*, *Allodesmus* + *Desmatophoca*). However, these placements range from weakly supported to very weakly supported. These specific fossil taxa incompletely preserve their postcrania. For many of these groups, excluding the aquatically-specialized pinnipeds and lutrines, few synapomorphies of the postcranial skeleton have been identified (Bryant et al., 1993; and the present study). Missing data may significantly alter the topological placement of a taxon if the only synapomorphies uniting it to its lineage are not codeable (see below for further discussion). The postcranial skeleton in arctoids, and carnivorans more broadly, displays strong biomechanical and ecological signals (Samuels et al., 2013), and thus may be more prone to homoplasy than other partitions, further complicating phylogenetic analyses of postcranial partitions.

Allodesmus and *Desmatophoca* have previously been identified as early-diverging otariids (Kellogg, 1922) or otarioids (Barnes, 1989; Barnes and Hirota, 1994; Furbish, 2015). It has been suggested the similarities between desmatophocines and otariids are the result of convergence upon fore-limb dominated swimming (Berta and Ray, 1990), a

notion corroborated by phylogenetic studies which have recovered desmatophocines as phocid relatives (Berta and Wyss, 1994; Deméré, 1994; Deméré and Berta, 2002).

Biomechanical studies have provided strong support for forelimb-dominated swimming in *Allodesmus* (Bebej, 2009; Pierce et al., 2011; Furbish, 2015), though only the latter attempted an ancestral state reconstruction using a phylogenetic framework integrating molecular data. Their findings support a monophyletic Otarioidea and a single origin of forelimb-dominated swimming at the base of the group (Furbish, 2015). The present postcranial-only analysis likely errs in identifying *Allodesmus* and *Desmatophoca* as diverging after *Thalassoleon*, though the allocation of Desmatophocidae to the otarioid family appears quite plausible.

Morphology data only by Parsimony Analysis

Character optimization indicates that *Kolponomos*' allocation to the pinnipedimorph branch, while well-supported, occurs despite a high number of reversals. *Kolponomos* appears to possess many odobenid character states, though it is unclear if these are phylogenetically-driven or the result of convergence upon a benthic feeding style. *Kolponomos* also displays numerous autapomorphies, and shares several character states exclusively with *Ailurus*, as well as several other character states that appear to deviate from the discrete character states of this analysis. Its peculiar morphology makes it difficult to align *Kolponomos* with any other arctoids, though its arctoid affinities are well-established (Stirton, 1960; Tedford et al., 1994; Kohno, 1996).

In a parsimony analysis, Boessenecker and Churchill (2013) identified five unequivocal synapomorphies of the Odobenidae, three of which are present in

Kolponomos (large, thick-margined, dorsoventrally-elliptical narial opening; dorsoventrally thick and laterally broad pterygoid strut; triple-rooted M¹), and two of which are not codeable for *Kolponomos*. Additionally, *Kolponomos* may possess the equivocal clade synapomorphy suggested in their analysis: the presence of well-developed cuspules on the P1-2 lingual cingulum, though the appearance and configuration of these cuspules in *Kolponomos* deviates from the typical odobenid form. Kohno (2006) identified another unambiguous synapomorphy of Odobenidae – antorbital process split by maxillary-frontal suture – that is absent in *Kolponomos*. *Kolponomos* also does not possess any of the proposed synapomorphies for crown pinnipeds. *Kolponomos* appears to have converged upon an *Odobenus*-like morphology, but may still have some bearing on early pinniped evolution. At the present moment, it is probably most appropriate to place it in Arctoidea *Incertae sedis*, until its postcrania or internal cranial architecture become available for study.

Total Evidence Analysis

Total evidence analyses (TEAs), while commonly applied to many other vertebrate groups (Larson and Dimmick, 1993; O’Leary, 1999; Schulte et al., 2003; Weksler, 2006; Maddin et al., 2012), have only recently begun to permeate the study of carnivorans (Finarelli, 2008; Churchill et al., 2014; Furbish, 2015; Wang et al., 2017). Molecular characters are often found to be more suitable than morphological characters in phylogenetic inference (Page and Holmes, 1998; Wake et al., 2011; Davalos et al., 2012; 2014; Springer et al., 2013; Zou and Zhang, 2016). Molecular characters are easily defined and coded, with four strictly-delineated, mutually-exclusive character states.

Differentiation of morphological data into discrete characters is made difficult by the greater integration of morphological structures (Olson and Miller, 1958; Cheverud, 1995). An important assumption of cladistics is the supposed independence of characters, but such rules are necessarily transgressed by morphological phylogenies (Riedl, 1978; Leamy et al., 1999; Cardini and Elton, 2008). However, molecular data alone offers little information on the details underlying the evolutionary history of a clade. In TEAs, the high proportion of molecular data constrains the topology by overwhelming the morphological data, so that morphological characters do not exert a strong influence on the phylogenetic position of those taxa with molecular data available. Rather, the morphological characters allow the lacunae of the lineages to be filled in by fossil taxa. If a topology or phylogenetic placement is accurate, fossils may offer direct evidence of ancestral states, break up long branches, and allow for accurate description of homoplasy.

The TEA in the present study produces a very unconventional topology that is highly unlikely, in light of fossil evidence (Deméré et al., 2003; Churchill and Boessenecker, 2014). The combined morphological and molecular dataset is unable to recover a similar topology to either the Total Morphology or Molecular datasets, which in isolation, produce reasonable, though highly discrepant topologies. This is most conspicuous on the pinniped branch, where Early and Middle Miocene taxa are observed towards the terminal nodes, and extant, highly derived taxa are recovered towards the stem of each group. An otariid-odobenid grouping is very well-supported by molecular data, but the TEA is not able to accommodate the fossil taxa into this clade without producing an illogical topology. *Prototaria* and *Proneotherium* are well-established early-diverging odobenids, connecting *Odobenus* to the base in the analyses of the

morphological partitions. However, the only fossil otariid included in the analysis, *Thalassoleon*, is already highly derived, as is *Pithanotaria*, another early-diverging otariid that is not as completely known, and was not included in the present study. *Eotaria* appears to represent a more conspicuous transitional form that would theoretically connect the otariids to the base of the tree, but this taxon is known only from isolated mandibles (Boessenecker and Churchill, 2015; Velez-Juarbe, 2017). Due to this fossil otariid gap, there is less morphological disparity between the aquatically-specialized crown otariids and *Odobenus* than between *Prototaria* and *Thalassoleon*. Consequentially, *Odobenus*, and later-diverging crown otariids, are forced towards the base of their respective branches. The same pattern is observed within the phocid clade, in which the middle Miocene fossil taxon *Devinophoca* appears as the latest-diverging phocid, and highly derived extant taxa are pushed toward the base.

Discussion

Pinnipedimorph Taxonomy

The Pinnipedimorpha was erected by Berta (1991) and includes *Enaliarctos* and all of its descendents, including a monophyletic crown-group Pinnipedia, which is strongly supported in all phylogenetic analyses performed in the present study. This study finds *Puijila* and *Potamotherium* to be members of this lineage that diverged prior to *Enaliarctos*, suggesting that a more inclusive subfamilial clade is warranted. All phylogenetic analyses in the current study recover a monophyletic group that includes crown group pinnipeds and the stem pinnipeds recognized here (*Puijila*, *Potamotherium*, *Kolponomos*, *Enaliarctos*, *Pteronarctos*, *Pinnarctidion*). A monophyletic Pinnipedia is

restricted to previously-recognized crown group pinnipeds in all analyses excepting the TEA, which also recovers *Puijila*, *Potamotherium*, *Kolponomos*, *Enaliarctos*, *Pteronarctos* and *Pinnarctidion* within the crown group. The discordant topologies between the TEA, the molecular-only analysis, and the morphological-only analyses suggest the molecular and the morphological data are highly incongruent. However, the strong support for a monophyletic *Puijila* + *Potamotherium* + Pinnipedimorpha in all phylogenetic analyses suggests *Puijila* and *Potamotherium* may confidently be identified as members of the lineage leading to pinnipeds.

Puijila and *Potamotherium* do not possess many of the conventional pinniped synapomorphies, but as potential stem pinnipedimorphs, they should not be expected to possess these features. The present Bayesian analyses suggest the features of modern pinnipeds arose sequentially, as observed in many other secondarily aquatic tetrapods (Hall 1999), rather than as an integrated package. Figure 2.9 displays the pinniped branch of the strict consensus tree from the parsimony analysis of the Total Morphology partition, with a molecular backbone constraint enforced, replete with a time scale to display the age ranges of fossil taxa.

Five unambiguous and 24 ambiguous synapomorphies were identified for a clade of *Potamotherium* + *Puijila* + pinnipedimorphs (Table 13). Unsurprisingly, it is the basicranial region that supports the phylogenetic affinities of *Puijila* and *Potamotherium*, as seven of these possible synapomorphies relate to the basicranial region. Unfortunately, data from the basicranial region is only incompletely known from many fossil specimens, as the majority of basicranial characters are not preserved or are difficult to access. As these regions are of significant phylogenetic utility, conclusions on the precise

phylogenetic relationships of early-diverging fossil pinnipeds may be reinterpreted once such data becomes available. Preservational biases have occasionally drastically misled identifications of fossil specimens (Donoghue and Purnell, 2009; Pattinson et al., 2015), and they can cause directional shifts in phylogenetic analyses (Sansom and Wills, 2013). Fossil specimens may appear to lack later derivations or specializations associated with more crown-ward clades, and thus, may erroneously be shifted toward the stem (Sansom, 2015).

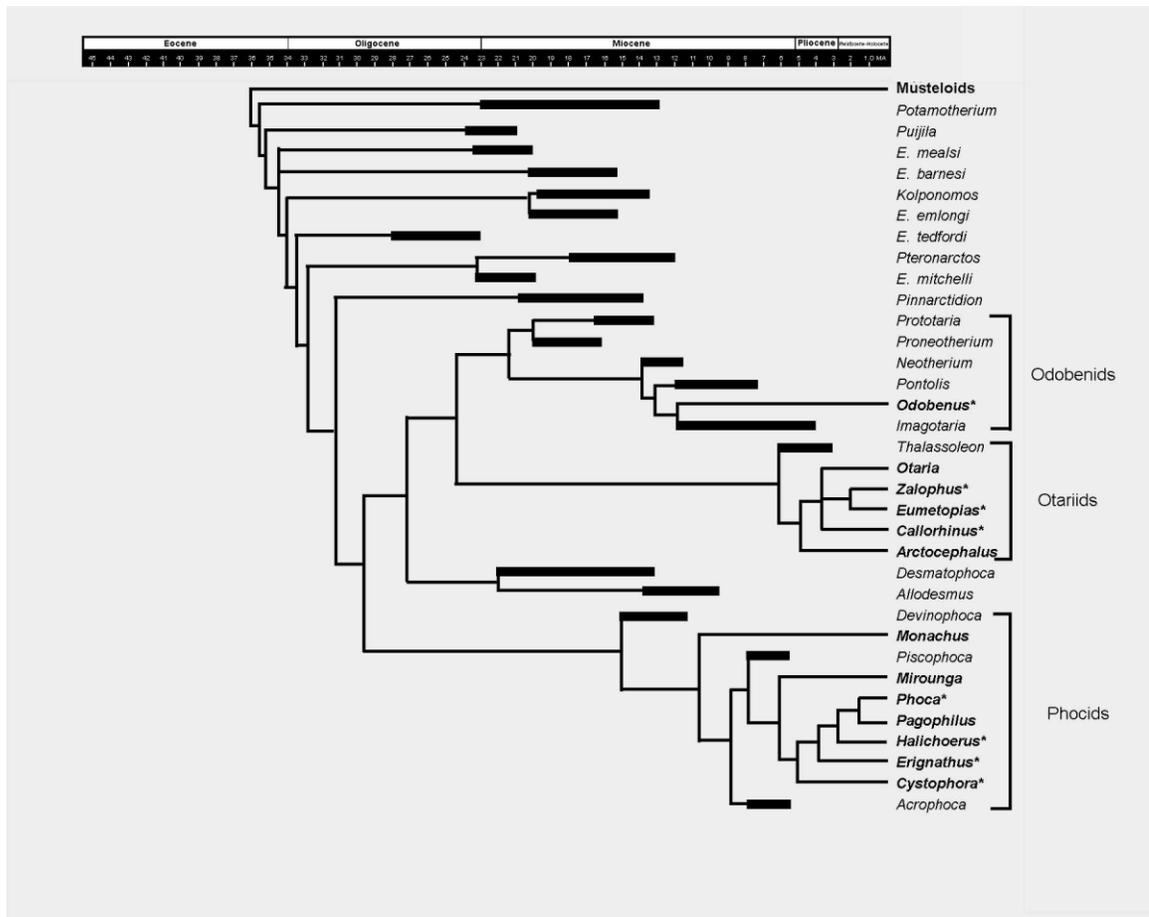


Figure 2.9. Pinniped branch of the strict consensus tree from the parsimony analysis of the Total Morphology partition with a molecular backbone enforced, with a geological time-scale. Black bars indicate known age ranges of fossil taxa (ranges shown include age uncertainty).

Many previous phylogenetic analyses identifying *Potamotherium* as a mustelid have apparently limited their observations to just a handful of specimens (Wyss, 1987; Bininda-Emonds and Russell, 1996; Wang, 2005; Finarelli, 2008) or relied on Savage's (1957) thorough description of the taxon (Furbish, 2015). The pinnipedimorph affinities of *Potamotherium* become increasingly apparent upon inspection of additional undescribed material of *Potamotherium* from the collections at NMB, MNHN, and FSL. *Potamotherium* displays several polymorphic characters, with the derived states commonly representing pinnipedimorph synapomorphies. The variable appearance of these pinnipedimorph synapomorphies suggests a transitional morphology between terrestrial arctoids and pinnipedimorphs. These features include: presence of large antorbital process; mandible deepest anteriorly; reduction of the fossa for the tensor tympani; presence of a palatal midline ridge.

Although the group Pinnipedimorpha is well-supported, the details of the evolution of the stem lineages may not be well-resolved. For example, there is considerable cranial and dental diversity between different species of *Enaliarctos* (Cullen et al., 2014; the present study), and significant taxonomic revision of the genus, with comparison to other stem pinnipeds overlapping *Enaliarctos* in age, may be warranted.

Despite superficially appearing less aquatically-specialized than *Potamotherium*, *Puijila* shares many traits with *Enaliarctos* to the exclusion of *Potamotherium*. Many of these traits are also observed in otarioids in general, but not phocids, including: a thin, projecting tympanic crest, an inflated and somewhat rounded caudal entotympanic, and presence of an alisphenoid canal. Specifically, the tympanic crest and tympanic bulla of *Puijila* strongly resemble those of *Enaliarctos emlongi* and *Enaliarctos mealsi*. In chapter

2 of the present work, we also identified the shared presence of an intrabullar septum in *Puijila*, *Enaliarctos emlongi*, and *Enaliarctos mealsi*. Additional traits found in *Puijila*, *Enaliarctos*, and later-diverging pinnipedimorphs, to the exclusion of *Potamotherium*, include: absence of I₁, a reduced M₁ metaconid, presence of sharp ventral keel on the axis, and presence of a cylindrical lesser tuberosity of the humerus.

The presence/absence of the alisphenoid canal has been nominated as a character of significant phylogenetic utility (Tedford, 1976; Koretsky, 2016). The alisphenoid canal carries multiple structures, including a branch of the external carotid artery, likely protecting it from occlusion during contraction of the pterygoideus muscle (Ewer, 1973). Accordingly, the alisphenoid canal may have been lost in taxa whose carotid canals lie closer to the orbit, so that the external carotid artery is only briefly exposed to the surrounding musculature. This is borne out by mustelids and mephitids, who display a reduced post-canine dentition, and in phocids, who possess large orbits. While it appears unlikely an organism could have lost the alisphenoid canal and subsequently regained it, we cannot, a priori, rule such a scenario out. Thus, the character was left unordered in our analysis, though we do admit a reversal to the presence of the canal is not very likely. Within the topology produced by the TEA, we can assume the loss of the alisphenoid canal represents an autapomorphy for *Potamotherium*, rather than a synapomorphy of a hypothetical *Potamotherium* + Phocidae clade (de Muizon, 1982; Koretsky and Rahmat, 2016). It is likely the alisphenoid canal was lost multiple times in arctoids, including at least once in phocids, mephitids, the clade containing mustelids + procyonids, and *Ailuropoda* respectively.

A more thorough investigation into the alpha and beta taxonomy of these early-diverging taxa may provide additional clues regarding the divergence of otariids and phocids, in the absence of incontestable transitional fossils.

Reappraisal of Pinniped Synapomorphies

Pinnipedia (Illiger, 1811) encompasses the last common ancestor of otarioids and phocids, and all of its descendants (Berta and Wyss, 1994). Wyss (1987) and Berta and Wyss (1994), suggested reversals were likely more common than convergence throughout the early evolutionary history of pinnipeds. This view was based on tree topologies in which Phocidae was recovered as the sister group to Odobenidae, and Ursidae was identified as the sister group to pinnipeds. Such a view has become less tenable as molecular analyses have revised our interpretation of these relationships. Many of these putative reversals may now be reinterpreted, in light of the present analysis. Reversals now appear less common than convergences within pinnipeds, a notion borne by the morphological characters of the early-diverging fossil representatives of the three extant pinniped families – *Prototaria* (or *Proneotherium*), *Eotaria*, and *Devinophoca*. In spite of their possession of odobenid, otariid, and phocid synapomorphies respectively, these taxa also possess a suite of primitive characters, lacking the aquatic specializations previously used to define Pinnipedia.

In light of the recent discovery of fossils attributable to *Prototaria*, *Proneotherium*, *Eotaria*, and *Devinophoca*, it appears that previously cited pinniped synapomorphies are more discrepant in distribution among crown group pinnipeds than previously believed, and may not define the base of Pinnipedia. Table 14 lists all

previously proposed synapomorphies of crown pinnipeds (Pinnipedia), and notes if the early-diverging fossil crown members of each pinniped family display the ancestral or derived character state. The ancestral state is observed at least once in a crown member for eleven of the sixteen characters. The five characters that do not display retention of an ancestral state are postcranial characters that are poorly sampled for these fossil taxa, many of which are only known from skulls, mandibles, and/or a few postcranial elements. The appearance of an ancestral state in any of these fossil forms could theoretically represent an anomalous derivation or reversal. However, if early-diverging representatives from more than one family retain the ancestral condition, then it is most parsimonious to assume the derived condition did not characterize the base of Pinnipedia. As Table 14 demonstrates, this latter scenario describes six of the sixteen characters. It must be assumed these numbers would increase if there were less missing data (44/80 total possible codings).

The following features have been used to delineate a monophyletic Pinnipedia to the exclusion of the stem “pinnipedimorphs” *Enaliarctos*, *Pteronarctos* and *Pacificotaria*: pit for tensor tympani absent; I³ lingual cingulum absent; M₁₋₂ trigonid suppressed; nasolabialis fossa absent; antorbital process large; P⁴ protocone shelf absent; P⁴ one- or two-rooted; M₂ absent (Berta and Wyss, 1994).

The absence of the pit for the tensor tympani does appear to be a synapomorphy of crown pinnipeds (Wyss, 1987; Berta and Wyss, 1994), as the tensor tympani appears to insert on the Eustachian canal in all extant pinnipeds sampled. However, Wesley-Hunt and Flynn (2005) identified a transitional state in *Pteronarctos*, in which the fossa for the tensor tympani is present, but only shallowly excavated into the promontory. Likewise,

the fossa for the tensor tympani is greatly reduced in *Puijila*, several specimens of *Potamotherium* (Mitchell and Tedford, 1973; Personal Observ.), and multiple species of *Enaliarctos* (Berta, 1991). CT data of the inner ear of early-diverging otariids, phocids, and odobenids should elucidate the timing of this transition to determine if the fossa for the tensor tympani was lost multiple times.

Lingual cingulum of the I³ is retained in *Prototaria* and *Thalassoleon*. An unreduced M₁ metaconid or trigonid is retained in *Eotaria*. The nasolabialis fossa appears to have been lost multiple times in pinnipeds, as it is present in a stem otariid (*Thalassoleon*), multiple fossil odobenids (*Proneotherium* and *Imagotaria*), and a possible desmatophocine (*Pinnarctidion*). Polarity for a large antorbital process must now be reversed, and the character can be conceived of as a possible synapomorphy for otarioids, with further derivation in both otariids and odobenids. A protocone shelf of the P⁴ is retained in *Devinophoca* and *Proneotherium*. Reduction of the number of roots of P⁴ (<3) appears to be a synapomorphy of pinnipeds, however, *Devinophoca* may display a transitional stage in which the posterior root is bilobed, though the roots are nevertheless well-merged (Koretsky and Holec, 2002: Fig.6). A similar P⁴ root morphology is observed in *Proneotherium* and *Neotherium*. The M₂ is retained in *Pontolis* (Deméré, 1994), *Eotaria* (Boessenecker and Churchill, 2013), and even atavistically reappears in extant otariids (Drehmer et al., 2004).

Of these proposed synapomorphies, only absence of the fossa for the tensor tympani and reduction of P⁴ roots appear to definitively define the node at the base of Pinnipedia. Berta and Wyss (1994) also listed a set of ambiguous postcranial synapomorphies of Pinnipedia, though their presence or absence in *Pteronarctos* and

several species of *Enaliarctos* cannot be asserted without postcranial remains. These are: five lumbar vertebrae present, flattened and posteriorly expanded olecranon process, expanded distal end of radius, pubic symphysis unfused, loss of fovea teres femoris, greater trochanter of femur lost. These synapomorphies have not been discovered in pinnipedimorphs, nor have the plesiomorphic conditions been identified in any fossil pinnipeds. However, some of these are approached by *Potamotherium* and *Enaliarctos*, who display somewhat expanded distal radii, somewhat expanded greater trochanters, and a reduced fovea teres femoris. Unsurprisingly, many of these features are thought to be related to aquatic adaptation – general flattening of the long-bones, posterior expansion of the olecranon process, loss of the fovea teres femoris - as they are observed homoplastically in other lineages of aquatic mammals (Gingerich et al., 1990; 1994).

Another more inclusive clade than the Pinnipedimorpha is also recognized – Pinnipediformes (Berta, 1994). This group encompasses *Pteronarctos* and Pinnipedia, to the exclusion of *Enaliarctos* (Berta, 1994). Four additional unambiguous synapomorphies were identified for Pinnipediformes: absence of lacrimal-jugal contact; maxilla contributes heavily to orbit; embrasure pit of P⁴- M¹ shallow or absent; mastoid process in close proximity to paroccipital process and connected by a ridge.

The extent of the lacrimal is difficult to ascertain in fossil pinnipeds and their ancestors, as the lacrimal becomes well-fused to surrounding bones in ontogeny. It appears likely this is a pinniped synapomorphy. The discovery of juvenile specimens displaying the presence or absence of a lacrimal in *Puijila* or *Enaliarctos* could confirm or undermine this contention. The maxillary contribution to the orbit is also likely a pinniped or pinnipediforme synapomorphy, but fusion of these elements in *Enaliarctos*

and *Puijila* precludes certain determination. While the embasure pit of *Proneotherium* is reduced (Boessnecker and Churchill, 2013), it is nevertheless present, while all extant pinnipeds observed lack an embasure pit outright. In phocids, the mastoid and paroccipital processes are widely separated, and the polarity of this character should be reversed, so it is considered a synapomorphy of otarioids.

Another proposed synapomorphy of Pinnipedia is the presence of prominent orbital vacuities (Wyss, 1987; Berta, 1991), which are unossified spaces on the medial orbital wall (Wyss, 1987). The presence of orbital vacuities appears to be unique to crown pinnipeds. The orbital vacuities are similar in phocids and otariids, but are placed far posteriorly in *Odobenus* (Kohn, 2006), though fossil walrus do possess a pinniped-like orbital vacuity (Deméré and Berta, 2001). Though similarly placed, the otariid orbital vacuity is of a different configuration than the phocid orbital vacuity (Wozencraft, 1989; Bininda-Emonds and Russell, 1996), and for that reason, Berta and Wyss (1994) speculate of an independent origin of orbital vacuities in the three pinnipeds families, a hypothesis supported by the present phylogenetic analysis. Orbital vacuities are absent in *Pinnarctidion*, present in *Allodesmus* (Berta and Wyss, 1994) and possibly incipient in *Desmatophoca* (Deméré and Berta, 2002).

Additional ambiguous synapomorphies of crown pinnipeds of Berta and Wyss (1994) include: enlarged tuberosities of the humerus; and a flattened and enlarged greater trochanter. A somewhat enlarged, though unflattened greater trochanter of the femur is observed in *Thalassoleon*. A somewhat enlarged lesser tubercle of the humerus that continues down the shaft as a cylindrical ridge, is observed in *Puijila*, *Semantor*, and the desmatophocines.

The earliest-diverging otariid (*Thalassoleon*) and phocid (*Devinophoca*) included in the analysis both display decidedly derived morphologies (Deméré and Berta, 2005; Koretsky et al., 2016). Yet, several character states previously believed to have been lost at the base of crown Pinnipedia are retained even in these derived taxa (Table 14). The earliest-diverging odobenid (Kohn, 1996; Boessencker and Churchill, 2013) displays only a single purported pinniped synapomorphy of Berta and Wyss (1994) – presence of the antorbital process – a character which is now identified as an otarioid synapomorphy, and the specific configuration of this character in *Prototaria* is more appropriately considered an odobenid synapomorphy (Berta and Wyss, 1994). Deméré and Berta (2002) commented on the lack of the fovea for the teres femoris in *Proneotherium*, suggesting it would be expected given its transitional morphology. However, as this was offered as a pinniped synapomorphy, it should theoretically be present in *Proneotherium*. It would not be unexpected for a transitional odobenid to lack odobenid synapomorphies, but it would be unconceivable to observe a transitional odobenid lacking several pinniped synapomorphies, considering how few synapomorphies are identified (Berta and Wyss, 1994).

From the results of the present study, we reject many of the synapomorphies previously used to diagnose Pinnipedia, as many were founded on hypotheses of sister group relationships of Pinnipedia-Ursidae and Phocidae-Odobenidae. However, we recognize a new suite of likely synapomorphies that support a monophyletic crown Pinnipedia, to the exclusion of *Enaliarctos* and *Pteronarctos*. Though the polarity of many characters previously recognized as pinniped synapomorphies has been reversed, the parsimony analysis of the Total Morphology partition, with a backbone constraint,

identifies two unambiguous synapomorphies, and 19 ambiguous synapomorphies of Pinnipedia (Table 12). None of these are basicranial characters, and only two are cranial, while the vast majority are postcranial (15/21), including the only two unambiguous synapomorphies. Admittedly, many of these possible synapomorphies can not, at the present time, be identified in early-diverging members of the crown families due to inadequate preservation, and may turn out to represent independent derivations. Also, several of these synapomorphies require reversals to the ancestral condition in *Prototaria*, *Proneotherium*, *Thalassoleon*, and/or *Devinophoca* (unambiguous synapomorphies 1, 3, 5, 13, 17 in Table 12), lessening the confidence with which we can assign them to the base of Pinnipedia. Furthermore, as with those identified by Berta and Wyss (1994), many of the synapomorphies identified here are uniquely approached by stem pinnipedimorphs, among arctoids. The stem pinnipedimorphs identified in the analysis appear to display a transitional or incipient state for many of these characters (ambiguous synapomorphies 6, 8, 13, 14, and 16, and both unambiguous synapomorphies in Table 12), suggesting selective pressures favouring those traits were already present in stem pinnipedimorphs.

Thus, while the present analysis identifies a suite of potential pinniped synapomorphies, an investigation of their distribution among fossil taxa indicates that several of these features appear to be incipiently present in stem pinnipeds and others may have arisen in parallel between the three extant pinniped families.

Parallel Evolution and Swimming Specialization in Arctoids

Swimming has evolved multiple times in arctoids (Berta et al., 2005). While no other known arctoids have developed the remarkable swimming specializations observed in pinnipedimorphs, many other taxa are considered to be semi-aquatic, including otters, the American mink, the European mink, the polar bear, the robust otter-like fossil musteloid *Mionictis* (Baskin, 1998), and, if its affinities lie outside the pinniped divergence, *Kolponomos*. Otters, minks and *Mionictis* all share with *Puijila* and *Potamotherium* a similar ectomorph bodyplan and several other features related to swimming and aquatic feeding, including webbed digits (Savage, 1957; Berta et al., 2005; Rybczynski et al., 2009). These features are so numerous that they have even previously been used to assert the lutrine affinities of *Mionictis* (known from the middle Miocene) (Baskin 1998; Tseng et al., 2009) and *Potamotherium*, though neither of these appear possible in the light of divergence time estimate studies consistently identifying a late Miocene divergence of Lutrinae (Sato et al. 2010). If these arctoid taxa could have converged upon similar specializations related to swimming, perhaps similar shifts could have begot flippers independently in otariids, phocids, and odobenids.

If *Enaliarctos* and *Pteronarctos*, both flippered taxa, are stem pinnipeds, this suggests the last common ancestor of crown pinnipeds was flippered. Even in this scenario, parallelisms still appear rampant within the three crown pinniped families. Most striking is the trend towards homodonty and reduction in the length of the tooth row (Boessenecker, 2011). The earliest phocid and odobenid known from cranio-dental material display heterodonty, though their carnassials are becoming assimilated and falling in file with the remaining postcanines (Kohno, 1996; Koretsky and Halec, 2002).

Enaliarctos, though it retains multicuspidate and disparately shaped postcanines, is trending toward a more homodont dentition. A transitional series, with regards to homodonty, can already be established within *Enaliarctos*, from the more heterodont *E. mealsi* and *E. barnesi*, to the nearly homodont *E. mitchelli* (Berta, 1991). Likewise, *Puijila* and *Potamotherium* display reduced molars, indicating a reduction of the tooth row. While reduction and/or loss of the M^2/M_2 also characterises neomustelids, the M^1 of mustelids is rarely as reduced, and is commonly larger than their premolars. The M^1 of *Puijila* and *Potatherium* is buccolingually narrow, and similar in size and shape to the M^1 observed in USNM 314295 (*Enaliarctos barnesi*). Evidently, selective pressures favouring homodonty were already affecting these early pinniped ancestors, as they became increasingly specialized for an aquatic existence.

While the dentition of *Enaliarctos* suggests a raptorial feeding style (Berta and Adam, 2002; Churchill and Clementz, 2015) in which the jaws and teeth are the only means of capturing prey (Hocking et al., 2017), its skeletal morphology suggests it was likely capable of manipulating its prey with its forelimbs (Berta and Ray, 1990; Hocking et al., 2017). It appears likely *Enaliarctos* still practiced, at least facultatively, though possibly habitually, a semi-aquatic feeding style (Hocking et al., 2017), in which the prey may be captured under water and consumed or processed at the surface or on land, as seen in many modern otter taxa. If *Enaliarctos* is emblematic of the hypothetical last common ancestor of crown pinnipeds, then crown pinnipeds ostensibly developed many of their extreme aquatic specializations in parallel. Hocking et al. (2017) suggests aquatic mammals are limited to a small number of feeding styles, partly dependent on their degree of aquatic adaptation. Within the framework of Hocking et al., (2017) *Enaliarctos*,

and other pinnipedimorphs may have employed both semi-aquatic and raptorial feeding styles. A transition to obligate raptorial feeding in such organisms would not be unsurprising. Such an event could have transpired as oceans cooled during the Miocene, when the earliest known fossil taxa confidently ascribed to Otariidae, Phocidae, and Odobenidae appear. Specializations associated with raptorial feeding in the crown pinniped families appear to have arisen independently in otariids and phocids, as suggested by the present data set, which identifies independent transitions towards homodonty in otariids and phocids (Figures 2-12 and Table 14). Convergent evolution of aquatic feeding behaviours and related morphologies within closely-related lineages has previously been documented in the fossil record of Ziphiidae (Cetacea) (Bianucci et al., 2016).

Adaptive radiations were thought to characterise the stem of pinnipedimorphs (Simpson, 1945), but recent evidence, based on tests of cranial disparity (Jones et al., 2016) and molecular markers (Higdon et al., 2007), suggest rapid radiations did not occur until the otarioid-phocoid split. Subsequent adaptive radiations appear to have taken place separately as otariids and odobenids diverged. This scenario is supported by the primitive morphologies of the early-diverging members of each extant pinniped family. Most notably, the early diverging odobenids *Prototaria* and *Proneotherium* do not depart significantly, in terms of morphology, from *Enaliarctos* and *Pteronarctos*.

Convergent physiological adaptations in marine mammals have also been well-documented (Peichl et al., 2001). Notably, Mirceta et al. (2013) identified convergent increases in myoglobin abundance and surface charge, variables that are well-correlated with increased diving depth, in several lineages of marine mammals, including pinnipeds.

Ancestral sequence reconstruction was used to estimate the myoglobin net surface charge of extinct species. *Enaliarctos* was estimated to have displayed a slight increase in this net surface charge compared to terrestrial carnivorans. *Enaliarctos*' estimated net surface charge was similar to that displayed by the sea otter, *Enhydra lutris*, suggesting *Enaliarctos* obligately exploited shallow-waters. Compared to *Enaliarctos*, taxa within Phocidae and Otariidae display significant increases in net surface charge, suggesting the lineages acquired their aquatic specializations independently.

Other molecular work (Wang et al., 2009; Zhou et al., 2015) has found evidence of genes that appear correlated with aquatic adaptation more broadly across marine mammals. However, convergent evolution of genes has been difficult to detect across marine mammal lineages. Parallel substitutions of functionally-enriched genes do not appear to occur more frequently between marine mammals than they do between marine and terrestrial mammals (Irwin and Arnason, 1994; Foote et al., 2015; Zhou et al., 2015). While convergent molecular evolution and convergent phenotypic evolution are both common phenomena, adaptive molecular convergence associated with phenotypic convergence is uncommon (Foote et al., 2015).

Though our phylogenetic analyses identify a number of possible synapomorphies of crown pinnipeds, it is not possible to ascertain whether or not these shared traits arose via common ancestry or due to similar selective pressures on closely-related groups of organisms. Modern cladistics methods are not infallible. While more reliable than phenetic interpretations, phylogenetic inference of morphological data remains imprecise, and thus, susceptible to systematic error. This limits the confidence we can have in topological placements from such studies, including the present study.

The Mk model has monopolized Bayesian inference of discrete morphological data. While it has been shown to be effective in simple data sets, it may not be able to accurately model morphological evolution. The Mk model employs a continuous-time Markov process running over finite state spaces (Klopfstein et al., 2015). A Markov process is conditioned only on the active state of the process. The past and future of the process are independent of the current state. Furthermore, the Markov process is also assumed to be at stationarity and time-reversible. A process attains stationarity when the current state ceases being dependent on the starting state. A process is time-reversible when its stochasticity does not become inconsistent or ill-defined if time is reversed.

The stationarity and time-reversibility of this Markov process prevents the Mk model from accounting for directional evolution. Directional evolution, one of the three modes of selection originally proposed by Darwin (1859), involves an extreme phenotype being favoured. Such selection is believed to be strong when an organism must adapt to a drastic and sudden shift in ecological pressures. Conceptually, directional selection would be a powerful propeller for an organism beginning to adapt to an aquatic existence. Conversely, in organisms that are secondarily aquatic, or highly specialized in some other manner, it should be unlikely, though not impossible, for organisms to revert to a less specialized form, under the assumptions of Dollo's Law (Gould, 1970).

Since the Mk model does not allow for the input of assumptions of directional selection, it is unlikely that parallel evolution would reveal itself in a topology using the Mk model. A priori assumptions of directional selection are indeed difficult to integrate into an evolutionary model, but successful work has been carried out on characterizing directional selection in molecular datasets (Merritt and Quattro, 2001; Creevey and

McInerney, 2002; Nielson, 2005; Kosiol et al., 2008; McClellan, 2013; Enard et al., 2014; Bloom, 2017), allowing directional selection to be integrated into models of molecular evolution (Huelsenbeck et al., 2006; Ronquist et al., 2012). Unfortunately, the non-objective nature of morphological characters and datasets, as outlined earlier in this chapter, makes it difficult to characterise directional selection as it relates to adaptive phenotypes. The extent of parallel evolution in pinnipeds may thus be greater than that suggested by the present study and others. It is possible that the extreme aquatic specializations characterizing extant pinnipeds, including flippers, developed in parallel in otariids, odobenids, and phocids, but our current phylogenetic methods are not capable of detecting such an event.

Conclusion

At present, evidence overwhelmingly favours a monophyletic origin of pinnipeds. However, otariids, odobenids, and phocids display a startling amount of parallel evolution, as many of their shared features are absent in the early-diverging fossil ancestors of each family. Within a monophyletic framework, we postulate that parallel evolution may be the mechanism explaining their specialization within the aquatic realm, particularly with regards to raptorial feeding and hydrodynamic locomotion. A definitive answer awaits fossil evidence and the advancement of morphological phylogenetic methods. In the mean-time, statistical tests of convergence (Muschick et al., 2012; Ingram and Mahler, 2013; Arbuckle et al., 2014) could be applied to cladistic data sets of arctoids, to further examine the likelihood of parallel evolution within pinnipeds.

Chapter 4: Conclusion

In the present study, the holotype skeleton of *Puijila darwini* was described and biomechanical analyses were performed to test hypotheses of the plesiomorphic swimming condition in pinnipeds (Chapter 2). The complete description of *Puijila* allowed it to be included in phylogenetic analyses, several of which were performed in Chapter 3, to better understand how *Puijila darwini* factors into discussions of pinniped origins. The phylogenetic analysis confirmed that several features shared between *Puijila* and other stem pinnipeds, uncovered in Chapter 2, were indeed synapomorphies of a *Puijila* + Pinnipedimorpha clade, confirming *Puijila*'s identity as a 'transitional pinniped' (Rybczynski et al., 2009). A review of synapomorphies defining crown group Pinnipedia, including those identified in the present study and previous phylogenetic analyses of pinnipeds (Wyss, 1987; Berta and Wyss, 1994) suggests many of the pinniped synapomorphies identified in Parsimony analyses may not actually define the base of Pinnipedia. Many purported synapomorphies are not present in early-diverging members of the three extant crown pinniped families – otariids, odobenids, and phocids – and many other synapomorphies are not known in these taxa due to incomplete fossils. Instead, it appears many features formerly used to define pinnipeds actually arose in parallel between otariids, odobenids and phocids. A review of other proxies attempting to gauge the tempo of evolution in pinnipeds provide further support for a high degree of parallel evolution in pinnipeds. At the present time, it is difficult to identify an evolutionary sequence resulting in the disparate swimming modes in phocids and otariids from a fully aquatic ancestor. As additional post-cranial remains of early-diverging fossil pinnipeds become uncovered, a combination of phylogenetic and biomechanical analyses

may reveal the intricacies behind the complex transition, or transitions, which allowed pinnipeds to take to the sea.

Appendices

Appendix A : Supplementary Figures

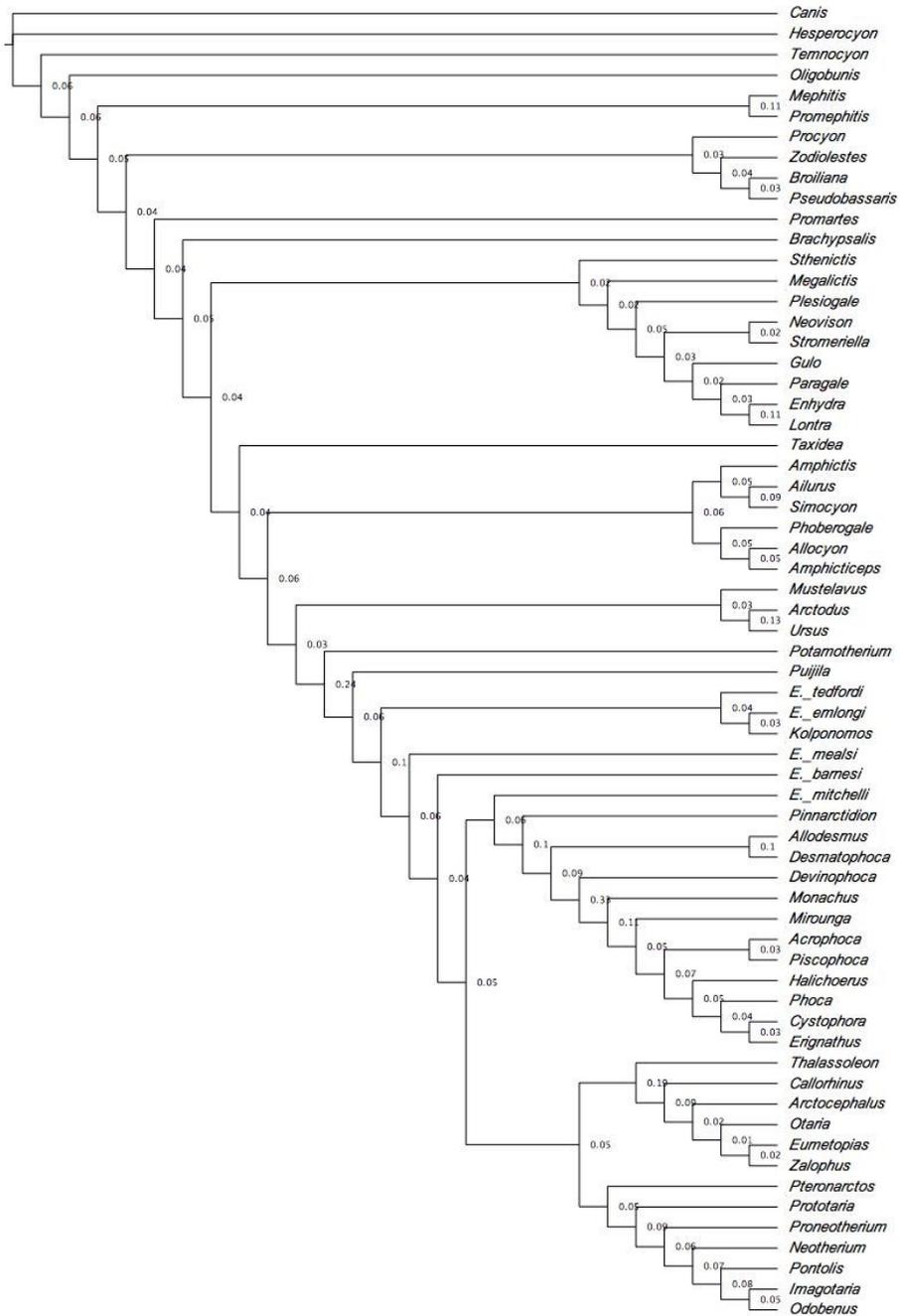


Figure A.1. Majority rule consensus tree of craniomandibular partition from Bayesian Inference

Analysis. Numbers at nodes are posterior probability values.

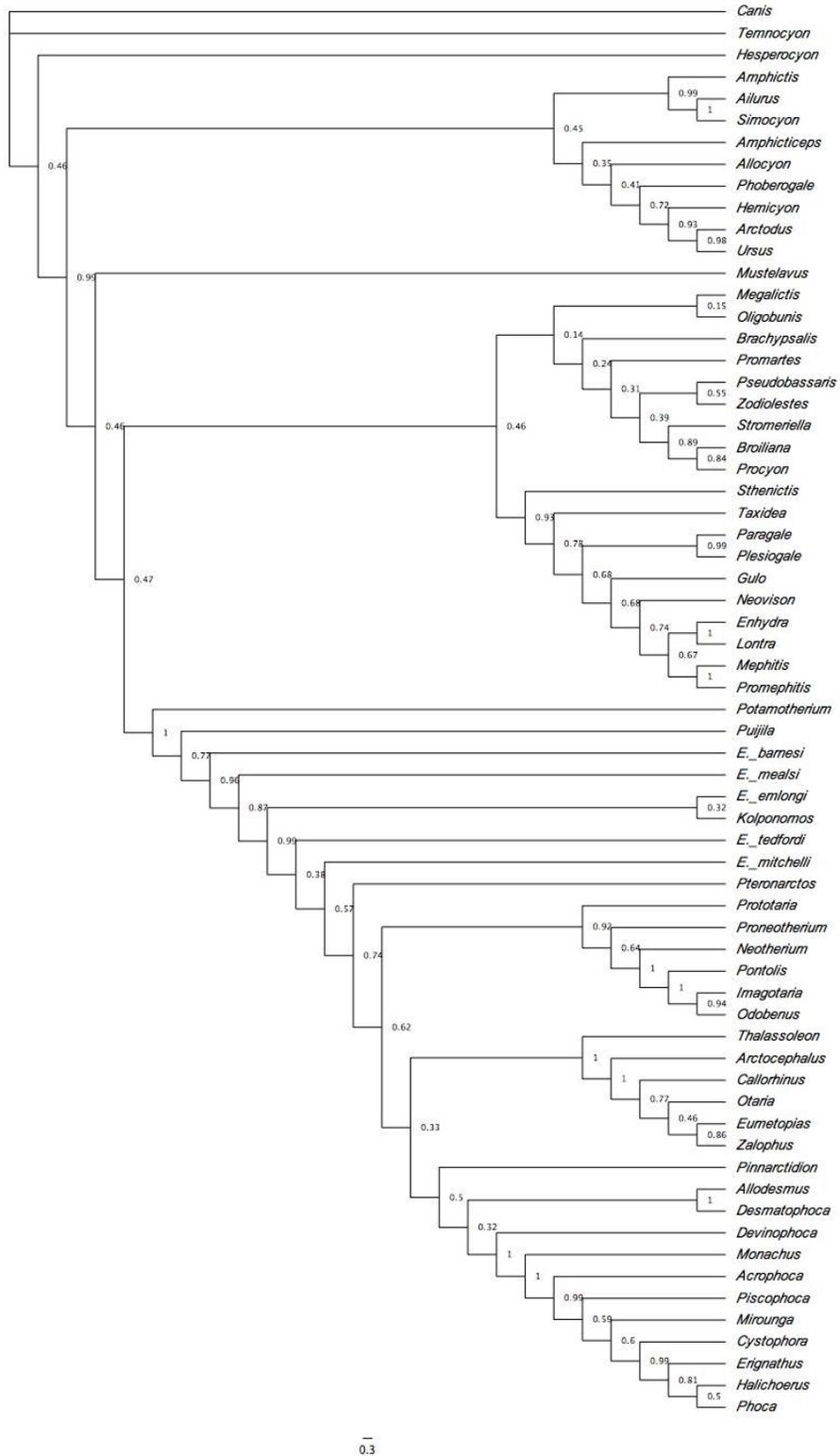


Figure A.2. Majority rule consensus tree of craniomandibular + dental partition from Bayesian Inference Analysis. Numbers at nodes are posterior probability values.

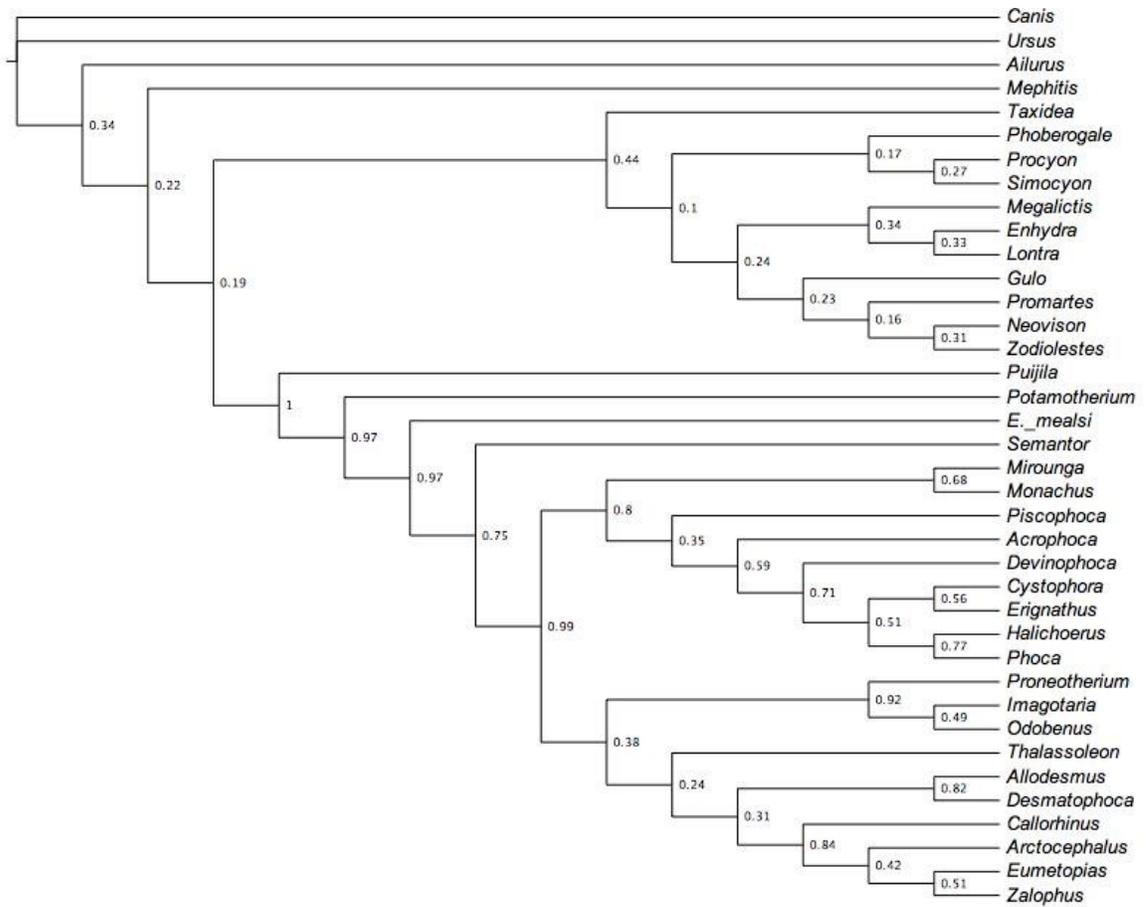


Figure A.3. Majority rule consensus tree of postcranial partition from Bayesian Inference Analysis.

Numbers at nodes are posterior probability values.

Majority-rule consensus tree

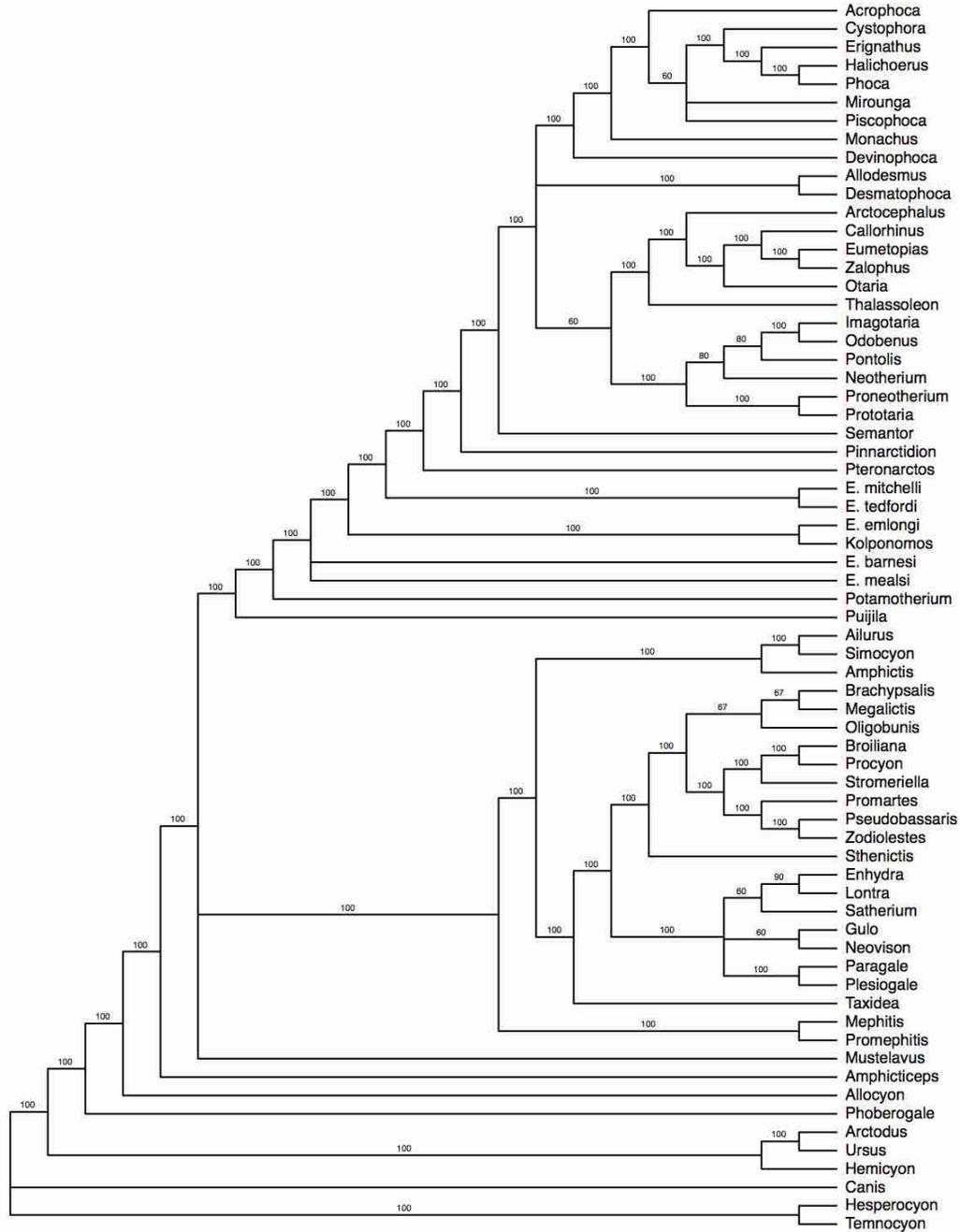


Figure A.5. 50% majority rule consensus tree from heuristic search of Total Morphology dataset with a molecular backbone constraint.

Majority-rule consensus tree

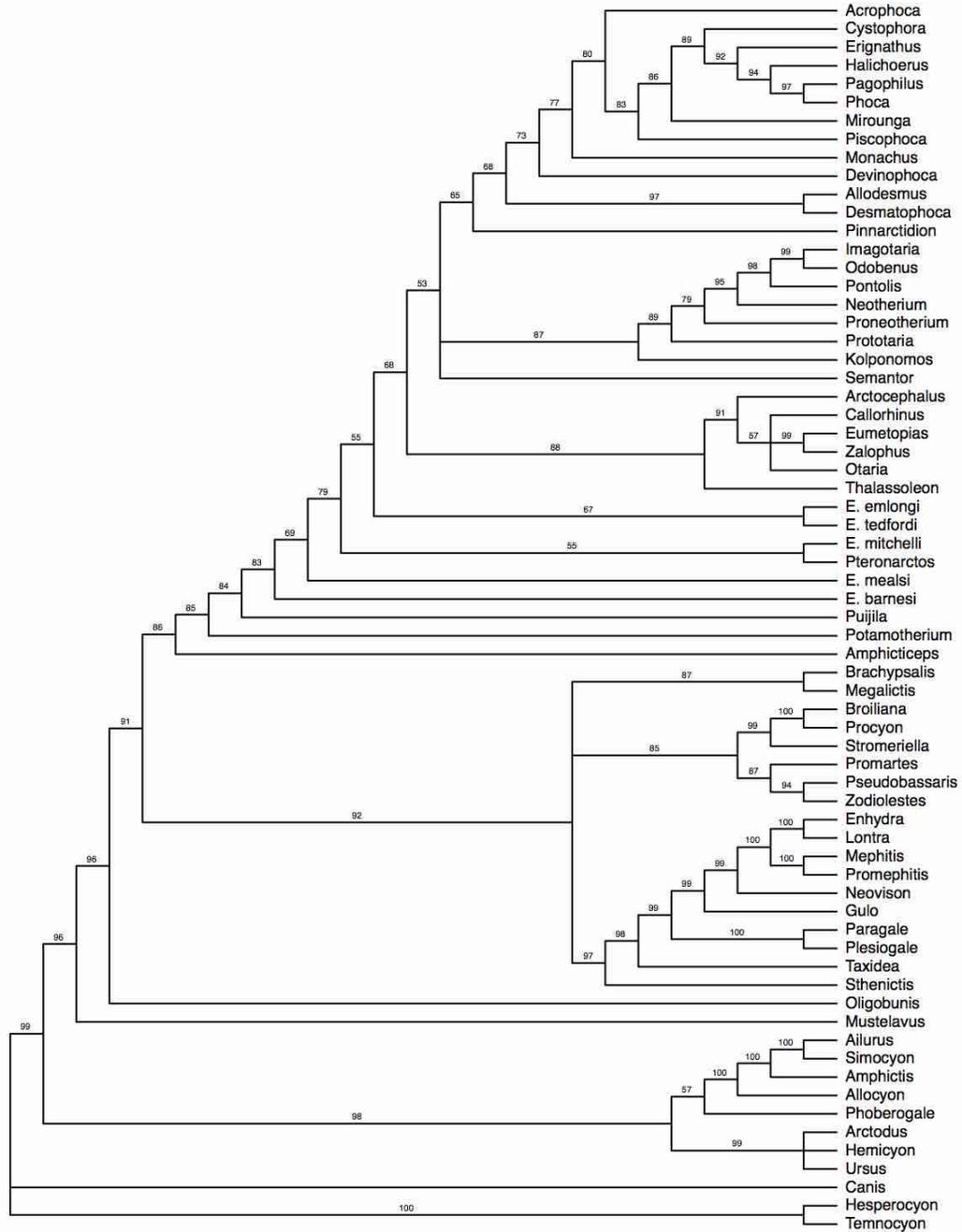


Figure A.6. 50% majority rule consensus tree from heuristic search of Craniomandibular + Dental

Only dataset without a molecular backbone constraint.

Majority-rule consensus tree

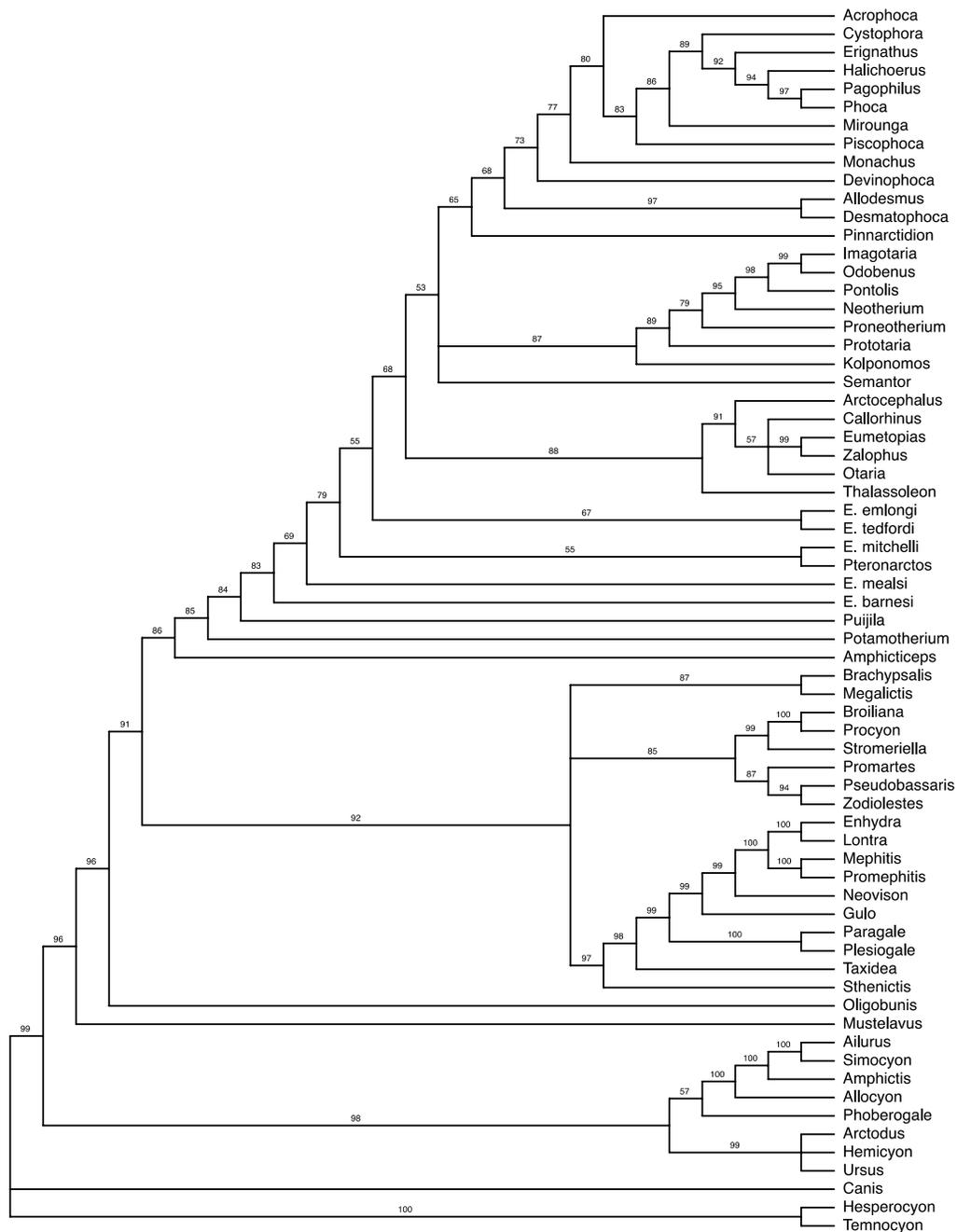


Figure A.7. 50% majority rule consensus tree from heuristic search of Craniomandibular + Dental
Only dataset with a molecular backbone constraint.

Appendix B : Tables

Table 1. List of specimens examined for the comparative description

Taxon	Specimen Number	Institution
<i>Acrophoca longirostrus</i>	USNM559323	USNM
<i>Acrophoca longirostrus</i>	USNM421632	USNM
<i>Allodesmus packardi</i>	USNM255527	USNM
<i>Allodesmus packardi</i>	USNM 205315	USNM
<i>Allocyon loganensis</i>	Cast of UCMP 24106	UCMP
<i>Amphicticeps shackelfordi</i>	AMNH 19010	AMNH
<i>Amphicticeps shackelfordi</i>	AMNH 19017	AMNH
<i>Desmatophoca brachycephala</i>	USNM 335451	USNM
<i>Desmatophoca oregonensis</i>	USNM 335246	USNM
<i>Desmatophoca oregonensis</i>	UOMNH F375	UOMNH
<i>Enaliarctos barnesi</i>	USNM 314295	USNM
<i>Enaliarctos emlongi</i>	USNM 250345	USNM
<i>Enaliarctos mealsi</i>	PAL 374272	USNM
<i>Enaliarctos mealsi</i>	FAM 117183	AMNH
<i>Enaliarctos mealsi</i>	PAL 374272	USNM
<i>Enaliarctos mitchelli</i>	USNM 175637	USNM
<i>Enaliarctos tedfordi</i>	USNM 206273	USNM
<i>Eumetopias jubatus</i>	20356	ROM
<i>Halichoerus grypus</i>	52829	CMN
<i>Imagotaria downsi</i>	USNM 335594	USNM
<i>Kolponomos newportensis</i>	PAL 215070	USNM
<i>Megalictis ferox</i>	FAM 25430	AMNH
<i>Megalictis ferox</i>	FAM 54079	AMNH
<i>Odobenus rosmarus</i>	5357	CMN
<i>Paragale hurzeleri</i>	PH 3638	NHMB
<i>Paragale hurzeleri</i>	MA 4641	NHMB
<i>Plesiogale angustifrans</i>	SG 28941	NHMB
<i>Potamotherium miocenicum</i>	1964 I 225	BSP
<i>Potamotherium miocenicum</i>	????	BSP
<i>Potamotherium valletoni</i>	1885 I 13	BSP
<i>Potamotherium valletoni</i>	1971 I 147	BSP
<i>Potamotherium valletoni</i>	SG836	NHMB
<i>Potamotherium valletoni</i>	SG 229	NHMB
<i>Potamotherium valletoni</i>	SG 226	NHMB
<i>Potamotherium valletoni</i>	SG4367	NHMB

<i>Potamotherium valletoni</i>	SG7624	NHMB
<i>Potamotherium valletoni</i>	SG7626	NHMB
<i>Potamotherium valletoni</i>	SG7622	NHMB
<i>Potamotherium valletoni</i>	SG 15087	NHMB
<i>Potamotherium valletoni</i>	SG 15088	NHMB
<i>Potamotherium valletoni</i>	SG7628	NHMB
<i>Potamotherium valletoni</i>	SG7627	NHMB
<i>Potamotherium valletoni</i>	SG15084	NHMB
<i>Potamotherium valletoni</i>	SG4405	NHMB
<i>Potamotherium valletoni</i>	SG4408	NHMB
<i>Potamotherium valletoni</i>	SG4414	NHMB
<i>Potamotherium valletoni</i>	SG4415	NHMB
<i>Potamotherium valletoni</i>	SG6987	NHMB
<i>Potamotherium valletoni</i>	SG6988	NHMB
<i>Potamotherium valletoni</i>	SG12352	NHMB
<i>Potamotherium valletoni</i>	SG20078	NHMB
<i>Potamotherium valletoni</i>	SG20080	NHMB
<i>Potamotherium valletoni</i>	SG20076	NHMB
<i>Potamotherium valletoni</i>	SG17987	NHMB
<i>Potamotherium valletoni</i>	SG8012	NHMB
<i>Potamotherium valletoni</i>	SG 8006-12	NHMB
<i>Proneotherium repenningi</i>	USNM 3355526	USNM
<i>Proneotherium repenningi</i>	USNM 335526	USNM
<i>Proneotherium repenningi</i>	USNM 206275	USNM
<i>Pteronarctos goedertae</i>	USNM 335432	USNM
<i>Semantor macrurus</i>	AMNH 100013	AMNH
<i>Thalassoleon mexicanus</i>	Cast of IGCU 902 (USNM 215020)	USNM

Table 2. Selected cranial measurements of NUFV-405 (*Puijila darwini*).

Cranial Measurements	(mm)
Cranium length	132.08
Width across antorbital processes	36.96
Width across supraorbital processes	27.86
Width of rostrum across canines	33.73
Auditory width	59.25
Mastoid width	70.88
Width of palate across anterior root of P ⁴	36.81
Width between infraorbital foramina	31.77
Transverse diameter of infraorbital foramen	5.9
Length of tooth row, C – M ²	47.58

Table 3. Selected measurements of the upper dentition of NUFV-405 (*Puijila darwini*).

Measurements of the upper dentition		(mm)
I ³	Length	6.09
	Width	3.57
C	Length	8.57
	Width	6.92
P ¹	Length	5.17
	Width	4.47
P ²	Length	7.27
	Width	4.66
P ³	Length	8.23
	Width	4.88
P ⁴	Length	11.36
	Width	8.82

M ¹	Length	5.69
	Width	10.12
M ²	Length	3.01
	Width	3.74

Table 4. Selected measurements of the mandible and lower dentition of NUFV-405 (*Puijila darwini*).

Measurements of the mandible and lower dentition		(mm)
Length of ramus		93.66
Length of toothrow, C – M ₂		53.16
Length of ramus below P ₃		17.74
P ₁	Length	5.57
	Width	4.31
P ₂	Length	6.85
	Width	3.93
P ₃	Length	7.66
	Width	4.55
P ₄	Length	9.15
	Width	4.68
M ₁	Length	10.71
	Width	5.11
M ₂	Length	4.37
	Width	3.87

Table 5. Selected measurements (mm) of the appendicular skeleton of NUFV-405 (*Puijila darwini*).

Humerus	
Greatest Length	97.96
Mid-shaft Mediolateral Diameter	8.54
Anteroposterior Diameter	15.32
Epicondylar Breadth	29.86
Supinator Wing Height	32.36
Ulna	
Greatest Length	97.32
Olecranon Length	19.74
Mid-shaft Mediolateral Diameter	4.89
Radius	
Greatest Length	74.52
Mid-shaft Mediolateral Diameter	8.42
MC-I	
Greatest Length	23.03
MC-II	
Greatest Length	30.60
MC-III	
Greatest Length	35.65
MC-IV	
Greatest Length	36.48
MC-V	
Greatest Length	28.00
Innominate	
Greatest Length	123.95
Femur	
Greatest Length	90.15
Length of Greater Trochanter	25.53
Mid-shaft Anteroposterior Diameter	9.49
Mid-shaft Mediolateral Diameter	9.49
Condylar Breadth	25.73

Tibia	
Greatest Length	110.79
Condylar Breadth	6.71
Fibula	
Greatest Length	100.60
Patella	
Greatest Length	13.91
Astragalus	
Greatest Length	19.40
Calcaneus	
Greatest Length	26.51
Cuboid	
Greatest Length	11.19
Navicular	
Greatest Length	9.87
MT-I	
Greatest Length	29.93
MT-II	
Greatest Length	38.44
MT-III	
Greatest Length	43.87
MT-IV	
Greatest Length	45.50
MT-V	
Greatest Length	37.72
Baculum	
Greatest Length	127.96

Table 6. Discriminant analysis structure matrix, eigenvalues, percent variance explained, and Wilk's k for each function. See Samuels et al., (2013) for a description of the indices.

Index	DF1	DF2	DF3
HEI	0.951	0.245	0.883
MANUS	-0.311	-0.091	-0.399
CLAW	-0.622	-0.666	.0611
FEI	0.789	-0.098	-1.048
TRI	-0.511	0.651	0.073
TSI	0.067	-0.950	0.015
PES	0.575	0.888	0.676
IM	0.129	0.538	0.358
Eigenvalues	3.283	1.255	0.654
% variance explained	56.2	21.5	11.2
Wilks' λ	0.036	0.154	0.348
X²	247.678	139.305	78.712
Canonical Correlation	.876	.746	.629

Table 7. Discriminant analysis classification matrix. 1=Arboreal, 2=Cursorial, 3=Generalist, 4=Scansorial, 5=Semi-fossorial, 6=Forelimb-dominated aquatic, 7=Hindlimb-dominated aquatic.

		Predicted Group						
Observed Group	% Correct	1	2	3	4	5	6	7
Arboreal	80	8	0	0	2	0	0	0
Cursorial	90	0	9	1	0	0	0	0
Generalist	40.7	5	7	11	3	1	0	0
Scansorial	72.7	0	0	2	8	1	0	0
Semifossorial	85.7	0	0	1	0	6	0	0
Forelimb-	50.0	0	0	2	1	0	3	0

dominated aquatic								
Hindlimb-dominated aquatic	83.3	1	0	1	0	0	0	10

Table 8. List of taxa included in each phylogenetic analysis.

Taxon	Molecular Only	Total Morphology	Cranio-mandibular	Cranio-mandibular + Dental	Dental Only	Post-cranial Only	Total Evidence Analysis
<i>Acrophoca</i>		√	√	√	√		√
<i>Ailurus</i>	√	√	√	√	√	√	√
<i>Allocyon</i>		√	√	√	√	√	
<i>Allodesmus</i>		√	√	√	√		√
<i>Amphictis</i>		√	√	√	√	√	
<i>Amphicticeps</i>		√	√	√	√	√	
<i>Arctocephalus</i>		√	√	√	√	√	√
<i>Arctodus</i>		√	√	√	√	√	
<i>Brachypsalis</i>		√	√	√	√	√	
<i>Broiliana</i>		√	√	√	√	√	
<i>Callorhinus</i>	√	√	√	√	√	√	√
<i>Canis</i>	√	√	√	√	√	√	√
<i>Cystophora</i>		√	√	√	√	√	√
<i>Desmatophoca</i>		√	√	√	√	√	√
<i>Devinophoca</i>		√	√	√	√	√	√
<i>E. barnesi</i>		√	√	√	√	√	
<i>E. emlongi</i>		√	√	√	√	√	
<i>E. mealsi</i>		√	√	√	√	√	√
<i>E. mitchelli</i>		√	√	√	√	√	
<i>E. tedfordi</i>		√	√	√	√	√	
<i>Enhydra</i>	√	√	√	√	√	√	√
<i>Erignathus</i>	√	√	√	√	√	√	√
<i>Eumetopias</i>	√	√	√	√	√	√	√
<i>Gulo</i>	√	√	√	√	√	√	√

<i>Halichoerus</i>	√	√	√	√	√	√	√
<i>Hemicyon</i>		√	√	√	√	√	
<i>Hesperocyon</i>		√	√	√	√	√	√
<i>Imagotaria</i>		√	√	√	√	√	√
<i>Kolponomos</i>		√	√	√	√	√	
<i>Lontra</i>	√	√	√	√	√	√	√
<i>Megalictis</i>		√	√	√	√	√	√
<i>Mephitis</i>	√	√	√	√	√	√	√
<i>Mirounga</i>		√	√	√	√		√
<i>Monachus</i>		√	√	√	√	√	√
<i>Mustelavus</i>		√	√	√	√	√	
<i>Neotherium</i>		√	√	√	√	√	
<i>Neovison</i>	√	√	√	√	√	√	√
<i>Odobenus</i>	√	√	√	√	√	√	√
<i>Oligobunis</i>		√	√	√	√	√	
<i>Otaria</i>		√	√	√	√	√	
<i>Paragale</i>		√	√	√	√	√	
<i>Phoberogale</i>		√	√	√	√	√	√
<i>Phoca</i>	√	√	√	√	√	√	√
<i>Pinnarctidion</i>		√	√	√	√	√	
<i>Piscophoca</i>		√	√	√	√		√
<i>Plesiogale</i>		√	√	√	√	√	
<i>Pontolis</i>		√	√	√	√		
<i>Potamotherium</i>		√	√	√	√	√	√
<i>Procyon</i>	√	√	√	√	√	√	√
<i>Promartes</i>		√	√	√	√	√	√
<i>Promephitis</i>		√	√	√	√	√	
<i>Proneotherium</i>		√	√	√	√	√	√
<i>Prototaria</i>		√	√	√	√	√	
<i>Pseudobassar</i>		√	√	√	√	√	
<i>Pteronarctos</i>		√	√	√	√	√	
<i>Puijila</i>		√	√	√	√	√	√
<i>Semantor</i>		√			√		√
<i>Simocyon</i>		√	√	√	√	√	√
<i>Sthenictis</i>		√	√	√	√	√	

<i>Taxidea</i>	√	√	√	√	√	√	√
<i>Stromeriella</i>		√	√	√	√	√	
<i>Temnocyon</i>		√	√	√	√	√	
<i>Thalassoleon</i>		√	√	√	√		√
<i>Ursus</i>	√	√	√	√	√	√	√
<i>Zalophus</i>	√	√	√	√	√	√	√
<i>Zodiolestes</i>		√	√	√	√	√	√

Table 9. Species and DNA sequences used in the phylogenetic analysis of molecular data and the total evidence analysis, and their GenBank accession numbers.

Family	Taxon	IRBP	RAG1	APOB	BRCA1	VWF
Ailuridae	<i>Ailurus fulgens</i>	AB188520	AB188525	AB193430	AB371329	AB371361
Canidae	<i>Canis lupus</i>	AB371351	AB371339	AB371312	AB371319	AB371351
Mephitidae	<i>Mephitis mephitis</i>	AB109331	AB109358	AB193406	AB371327	AB371359
Mustelidae	<i>Enhydra lutris</i>	AB082978	AB109355	AB193403	AB285343	AB285389
	<i>Gulo gulo</i>	AB082962	AB109340	AB193407	AB285344	AB285390
	<i>Lontra canadiensis</i>	AB285373	AB285381	AB285335	AB285345	AB285391
	<i>Neovison vison</i>	AB082977	AB109354	AB193421	AB285367	AB285413
	<i>Taxidea taxus</i>	AB285379	AB285387	AB285341	AB285368	AB285414
Odobenidae	<i>Odobenus rosmarus</i>	DQ205892	GU167543	GU167634		JN415047
Otariidae	<i>Callorhinus ursinus</i>	AB188516	AB188521	AB193422	AB371323	AB371355
	<i>Eumetopias jubatus</i>	AB188517	AB188522	AB193423	AB371324	AB371356
	<i>Zalophus californianus</i>	AB365083	AB302263	GU167687		
Phocidae	<i>Cystophora cristata</i>	GU167468	GU167840	GU167686		
	<i>Erignathus barbatus</i>	DQ205894	GU167841			
	<i>Halichoerus grypus</i>	DQ205902	GU167843	GU167689		
	<i>Phoca vitulina</i>	AB188518	AB188523	AB193425	AB371326	AB371358

Procyonidae	<i>Procyon lotor</i>	AB082981	AB109359	AB193427	AB285371	AB285417
Ursidae	<i>Ursus arctos</i>	AB109333	AB109361	AB193429	AB371321	AB371353

Table 10. Marginal likelihood scores for each evolutionary model considered for each data partition used in the phylogenetic analysis. Selected models are in bold.

1) VWF
a. GTR invgamma, Run1=-4615.22, Run2=-4615.33
b. F81, Run1=-4504.10, Run2=-4504.71
c. HKY, Run1=-4299.11, Run2=-4298.79
d. HKY gamma, Run1=-4299.92, Run2=-4300.25
e. JC, Run1=-4516.66, Run2=-4515.44
f. SYM, Run1=-4316.94, Run2=-4315.33
g. GTR gamma, Run1=-4294.73, Run2=-4295.07
2) RAG1
a. F81, Run 1=-3548.40, Run2=-3548.66
b. GTR, invgamma, Run1=-3344.64, Run2=-3344.57
c. HKY, Run1=-3449.65, Run2=-3449.76
d. JC, Run 1=-3539.31, Run2=-3539.49
e. SYM, Run1=-3428.2, Run2=-3428.21
f. GTr gamma, Run1=-3348.07; Run2=-3348.08
3) APOB
a. F81, Run1=-2902.92, Run2=-2902.79
b. GTR invgamma=-2803.86, Run2=-2804.15
c. HKY, Run1=-2817.36, -2817.33
d. JC, Run1=-2917.18, Run2=-2917.05
e. SYM, Run1=-2842.27, Run2=-2842.39
f. GTR gamma, Run1=-2803.85, -2803.79
4) IRBP
a. F81, Run1=-4187.26, Run2=-4187.06
b. GTR invgamma run1=-3965.25, -3965.21
c. HKY, Run1=-4040.17; Run2=-4040.26
d. JC, Run1=-4212.26, Run2=-4212.34
e. SYM, Run1=-4079.6, Run2=-4079.55
f. GTR gamma Run1=-3966.70, Run2=-3966.91
5) BRCA1
a. F81, Run1=-5058.31, Run2=-5058.21
b. GTR, invgamma, Run1=-4919.49, Run2=-4919.93
c. HKY, Run1=-4927.22, Run2=-4927.83
d. HKY gamma, Run1=4923.83, Run2=-4924.20
e. JC, Run1=-5096.78, Run2=-5096.45
f. SYM, Run1=-4960.94, Run2=-4960.59
g. GTR gamma, Run1=-4915.16, Run2=-4915.24
6) Morphological
a. Gamma Run1=-4151.31, Run2=-4151.85

b. InvGamma, Run1=-4209.63, Run2=-4211.14
c. Standard Run1=-4207.77; Run2=-4210.80

Table 11. List of references which were used to supplement our first-hand observations of specimens.

Genus	Reference(s)
<i>Allocyon</i>	Merriam, 1930
<i>Amphicticeps</i>	Wang et al., 2005
<i>Amphictis</i>	Riggs, 1898
<i>Devinophoca</i>	Koretsky et al., 2002; Koretsky et al., 2015; Rahmat and Koretsky, 2016
<i>Enaliarctos</i>	Berta and Ray, 1990; Berta, 1991; Berta and Wyss, 1994
<i>Hadrokirus</i>	Amson and Muizon, 2014
<i>Hemicyon</i>	Colbert, 1941
<i>Hesperocyon</i>	Wang, 1994
<i>Kolponomos</i>	Stirton, 1960; Tedford et al., 1994
<i>Megalictis</i>	Valenciano et al., 2016
<i>Mustelavus</i>	Wang et al., 2005
<i>Neotherium</i>	Boessenecker and Churchill, 2013
<i>Phoberogale</i>	Ginsburg and Morales, 1995; De Bonis 2013
<i>Pinnarctidion</i>	Berta, 1994b
<i>Potamotherium</i>	Savage, 1957;
<i>Promephitis</i>	Geraads and Spassov, 2016
<i>Proneotherium</i>	Kohn et al., 1995; Demere et al., 2001
<i>Prototaria</i>	Kohn, 1994
<i>Pseudobassarlis</i>	Wang et al., 2005
<i>Pteronarctos</i>	Berta, 1994a
<i>Simocyon</i>	Wang, 1997; Salesa et al., 2008
<i>Temnocyon</i>	Hunt, 2011
<i>Thalassoleon</i>	Churchill and Boessenecker, 2014

Table 12. List of synapomorphies identified from the parsimony analysis of the Total Morphology dataset, with a backbone enforced, for crown pinnipeds.

Ambiguous
1. Fossa muscularis 1->0
2. Premaxilla-Maxilla Nasal Contact 0->1
3. P4/M1 Relative Size 1->0
4. M1 Metacone vs Paracone 1->0
5. Premolar Size 0->1
6. M1 metaconid 0->1
7. Neural Foramen Size 0->1
8. Lumbar Vertebrae Size 0->1
9. Ulna Olecranon Process 0->1
10. Metapodials/Phalanges, Keeled Heads 0->1
11. Manus Fifth Phalanx 0->1
12. Pubic Symphysis Fusion 0->1
13. Femur, ligamentum teres femoris 0->1
14. Fibula, Processus lateralis 0->1
15. Scapholunar, head of sesamoid process 1->0
16. Distal termination of trochlea 1->2
17. Tibia-Fibula Fusion 0->1
18. Cuboid, distal ectocuneiform facet 1->0
19. Humerus, Supinator Ridge 0->1
Unambiguous
1. Tail 0->1
2. Femur – Trochanteric Fossa 0->1

Table 13. List of synapomorphies identified from the parsimony analysis of the Total Morphology dataset, with a backbone enforced, for a clade including Puijila and all of its descendants.

Ambiguous
1. Anterior Palatine Foramina 0->1
2. Incisive Foramina 1->0
3. IOF 2->3
4. Postglenoid foramen 0->1
5. Epitympanic sinus 0->3
6. Posterior lacerate foramen 0->1
7. Petrosal connection 0->1
8. P4 accessory cusps 2->1
9. Humerus greater tubercle 1->0
10. Radius pronator teres process 0->2

11. Ulna coronoid process 0->1
12. Metacarp vs phalanges 0->1
13. Ilium length 0->1
14. Femur greater trochanter height 0->1
15. Femur fossa anterior to trochlea 0->1
16. Femur condylar angle 0->1
17. Tibia grooves 0->1
18. Astragalar groove 0->1
19. Calcaneum groove for gastrocnemius 0->1
20. Cuboid distal ectocuneiform facet 0->1
21. Scapholunar head of sesamoid 0->1
22. M1 hypocone 0->1
23. Pseudosylvian sulcus 0->1
24. P4 m1 size 0->1
Unambiguous
1. Postorbital Constriction 0->1
2. Round Window Size 0->1
3. P4 Protocone 0->7
4. M2 Location 0->1
5. M1 metaconid mesiodistal position 0->1

Table 14. The distribution of previously proposed pinniped synapomorphies (Berta and Wyss, 1994) across a selection of early-diverging fossil pinnipeds.

Previously proposed pinniped synapomorphies	<i>Enaliarctos</i>	<i>Prototaria</i>	<i>Proneotherium</i>	<i>Thalassoleon</i>	<i>Eotaria</i>	<i>Devinophoca</i>
Loss of pit for tensor tympani¹	0	?	0	?	?	?
I³ Lingual Cingulum¹	0	0	1	0	?	1
Reduced m1 metaconid¹	0	?	1	?	0	?
Nasolabialis Fossa Absence¹	0	0	0	0	?	1
Fossa muscularis absence¹	0	0	1	1	?	1
Antorbital Process Large¹	0	1	1	1	?	0

P⁴ Protocone Shelf¹	0	0	0	1	?	0
P⁴ 1- or 2-rooted¹	0	0	0	1	?	0
m2 absence¹	0	0	0	1	0	1
Five Lumbar Vertebrae¹	0	?	?	?	?	?
Olecranon flattened and expanded¹	0	?	?	1	?	1
Radius, expanded distal half¹	0	?	?	1	?	?
Pubic symphysis unfused¹	0	?	?	1	?	?
Fovea for teres femoris¹	0	?	0	1	?	1
Greater femoral trochanter larger and flattened¹	0	?	1	1	?	1
Tibia-Fibula Fusion¹	0	?	0	0	?	?

Table 15. List of specimens examined for the phylogenetic analysis.

Taxon	Specimen Number	Institution
<i>Acrophoca</i>	USNM421632	USNM
<i>Acrophoca</i>	SAS 563	MNHN
<i>Acrophoca</i>	MNHN SAS563	AMNH
<i>Acrophoca</i>	USNM559323	USNM
<i>Acrophoca longirostrus</i>	SAS 1654	MNHN
<i>Acrophoca longirostrus</i>	SAS 252	MNHN
<i>Acrophoca longirostrus</i>	SAS 1654	MNHN
<i>Aelurocyon brevifacies</i>	P12153 and P26051	FM
<i>Aelurocyon brevifacies</i>	FAM 12881	AMNH
<i>Ailuropoda</i>	ROM 33-10-30-17	ROM
<i>Ailuropoda</i>	ROM 35-1-20-1	ROM

<i>Ailurus fulgens</i>	ROM 91448 PM 8168	ROM
<i>Ailurus fulgens</i>	ROM 111047 PM 15819	ROM
<i>Allodesmus packardi</i>	USNM255527	USNM
<i>Allodesmus</i>	USNM 171108	USNM
<i>Allodesmus</i>	USNM 205315	USNM
<i>allodesmus</i>	USNM 23249	USNM
<i>Allodesmus kelloggi</i>	AMNH 32763	AMNH
<i>Amphicticeps shackelfordi</i>	AMNH 19010	AMNH
<i>Amphicticeps shackelfordi</i>	AMNH 19017	AMNH
<i>Amphictis ambiguus</i>	QU B 410	NHMB
<i>Amphictis ambiguus</i>	QU C 2	NHMB
<i>Angustictis mayri</i>	1937 II 13272	BSP
<i>Angustictis mayri</i>	1937 II 13263	BSP
<i>Angustictis mayri</i>	1937 II 13281	BSP
<i>Angustictis mayri</i>	1937 II 13701	BSP
<i>Angustictis mayri</i>	1937 II 13700	BSP
<i>Arctocephalus pusillus</i>	ROM 94946	ROM
<i>Arctocephalus pusillus</i>	ROM 56450	ROM
<i>Arctocephalus pusillus</i>	ROM 112999	ROM
<i>Arctocephalus pusillus</i>	ROM 112780	ROM
<i>Arctodus simus</i>	28299	CMN
<i>Bassariscus astutus</i>	ROM 30397	ROM
<i>Bassariscus astutus</i>	ROM 91-10-1-1	ROM
<i>Bathygale lemanensis</i>	213853	FSL
<i>Bathygale lemanensis</i>	????	FSL
<i>Bathygale lemanensis</i>		FSL
<i>Bathygale lemanensis</i>	SG 3215	MNHN
<i>Bathygale lemanensis</i>	SG3218	MNHN
<i>Bavarictis gaimerseimensis</i>	1952 II 5	BSP
<i>Bavarictis gaimerseimensis</i>	1952 II 3336	BSP
<i>Bavarictis gaimerseimensis</i>	1952 II 8	BSP
<i>Bavarictis gaimerseimensis</i>	1952 II 6	BSP
<i>Bavarictis gaimerseimensis</i>	1952 II 7	BSP
<i>Brachypsalis</i>	AMNH 27431	AMNH
<i>Brachypsalis</i>	P25615	FM
<i>Brachypsalis</i>	AMNH 27424	AMNH
<i>Brachypsalis</i>	FAM144533	AMNH
<i>Brachypsalis</i>	FAM144530	AMNH

<i>Brachypsalis</i>	FAM144570	AMNH
<i>Brachypsalis</i>	FAM144531	AMNH
<i>Brachypsalis</i>	FAM144541	AMNH
<i>brachypsalis</i>	FAM144532	AMNH
<i>Brachypsalis</i>	FAM144542	AMNH
<i>Brachypsalis</i>	FAM144546	AMNH
<i>Broiliana nobilis</i>	1937 II 13525	BSP
<i>Broiliana nobilis</i>	1937 II 13524	BSP
<i>Broiliana nobilis</i>	1937 II 13555	BSP
<i>Broiliana nobilis</i>	1937 II 13532	BSP
<i>Broiliana nobilis</i>	1937 II 13528	BSP
<i>Broiliana nobilis</i>	1937 II 14493	BSP
<i>Broiliana nobilis</i>	1937 II 13167	BSP
<i>Broiliana nobilis</i>	10356	BSP
<i>Callorhinus</i>	NMC A20764	CMN
<i>Callorhinus alascanus</i>	NMC 17024	CMN
<i>Callorhinus alascanus</i>	NMC 17023	CMN
<i>Callorhinus ursinus</i>	ROM 91483	ROM
<i>Callorhinus ursinus</i>	USNM 258588	USNM
<i>Campylocynodon personi</i>	YPM PU 17795	YPM
<i>Cephalogale</i>	MA7701-2	NHMB
<i>Cephalogale</i>	SG 20150-3	NHMB
<i>Cephalogale</i>	MA 2882	NHMB
<i>Cephalogale</i>	MA 7698	NHMB
<i>Cephalogale</i>	MA 7699	NHMB
<i>Cephalogale</i>	SG 7157	NHMB
<i>Cephalogale cadurcensis</i>	YPM PU 11446	YPM
<i>Cephalogale cadurcensis</i>	YPM PU 11444	YPM
<i>Cephalogale cadurcensis</i>	YPM PU 11445	YPM
<i>Cephalogale depereti</i>	MA7700	NHMB
<i>Cephalogale depereti</i>	SG 358/359	MNHN
<i>Cephalogale geoffroyi</i>		
<i>Cephalogale gracile</i>	SG 10744	NHMB
<i>Cephalogale gracile</i>	SG 365	MNHN
<i>Cephalogale minor</i>	BSP 1879 XV 733	BSP
<i>Cephalogale sp</i>	1952 II 4	BSP
<i>Cephaogale minor</i>	YPM PU 11458	YPM
<i>Cephaogale minor</i>	YPM PU 23654	YPM

<i>Cystophora cristata</i>	37055	CMN
<i>Cystophora cristata</i>	Z-766	CMN
<i>Daphoenus hartshovianus</i>	1971 I 148	BSP
<i>Desmatophoca brachycephala</i>	USNM 335451	USNM
<i>Desmatophoca oregonensis</i>	PAL 250283	USNM
<i>Desmatophoca sp</i>	USNM 335246	USNM
<i>Devinophoca claytoni</i>	USNM 415624	USNM
<i>Devinophoca emryi</i>	"USNM" 553687	USNM
<i>Enaliarctine</i>	USNM 335376	USNM
<i>Enaliarctos</i>	USNM 250345	USNM
<i>Enaliarctos emlongi</i>	USNM 250345	USNM
<i>Enaliarctos emlongi</i>	USNM 250345	USNM
<i>Enaliarctos barnesi</i>	USNM 314295	USNM
<i>Enaliarctos emlongi</i>	USNM 250345	USNM
<i>Enaliarctos mealsi</i>	PAL 374272	USNM
<i>Enaliarctos mitchelli</i>	USNM 175637	USNM
<i>Enhydrocyon n. sp.</i>	JODA 6222	JODA
<i>Enhydrocyon stenocephalus</i>	JODA 3795	JODA
<i>Enhydrocyon stenocephalus</i>	JODA 10777	JODA
<i>Erignathus barbatus</i>	75237	
<i>Eumetopias jubatus</i>	ROM 20356	ROM
<i>Franconictis</i>	1937 II 13571	BSP
<i>Franconictis</i>	1937 II 13572	BSP
<i>Franconictis</i>	1937 II 13536	BSP
<i>Franconictis</i>	1937 II 13236	BSP
<i>Franconictis</i>	1937 II 14963	
<i>Gulo gulo</i>	Vert 75400	CMN
<i>Gulo gulo</i>	NMC 44061	CMN
<i>Hadrokirus</i>	SAS 16276	MNHN
<i>Halichoerus</i>	AMNH 101483	
<i>Halichoerus grypus</i>	75481	CMN
<i>Halichoerus grypus</i>	Z-144	CMN
<i>Halichoerus grypus</i>	Z-903	CMN
<i>Halichoerus grypus</i>	52829	CMN
<i>Hemicyon sansaniensis</i>	SEP 54 a/b	MNHN
<i>Hemicyon sansaniensis</i>	SEP140	MNHN
<i>Hemicyon sansaniensis</i>	SEP149	MNHN
<i>Hesperocyon gregarius</i>	NMC 8753	CMN

<i>Hesperocyon gregarius</i>	1971 I 142	BSP
<i>Imagotaria downsi</i>	USNM 184061	USNM
<i>Imagotaria downsi</i>	USNM 23859	USNM
<i>Imagotaria downsi</i>	USNM 175439	USNM
<i>Imagotaria downsi</i>	USNM 335594	USNM
<i>Imagotaria downsi</i>	USNM 335564	USNM
<i>Imagotaria downsi</i>	USNM 184085	USNM
<i>Imagotaria downsi</i>	USNM 23867	USNM
<i>Imagotaria downsi</i>	USNM 23862	USNM
<i>Indarctos oregonensis</i>	JODA 15273 (Cast of UCMP 22362)	JODA
<i>Indarctos oregonensis</i>	JODA 10841 (Cast of 22362)	JODA
<i>Indarctos oregonensis</i>	UCMP 22461	JODA
<i>Indarctos oregonensis</i>	UCMP 22362	JODA
<i>Kolponomos newportensis</i>	PAL 215070	USNM
<i>Leptarctus oregonensis</i>	UO 35458	JODA
<i>Lontra canadiensis</i>	1971 I 140	BSP
<i>Megalictis ferox</i>	P12125	FM
<i>Mephitis mephitis</i>	Vert 75189	CMN
<i>Mephitis mephitis</i>	Vert 75057	CMN
<i>Mesocyon</i>	JODA 1210	JODA
<i>Mesocyon</i>	JODA 3082	JODA
<i>Mesocyon brachyops</i>	JODA 2875	JODA
<i>Mesocyon coryphaeus</i>	JODA 3366	JODA
<i>Mesocyon sp.</i>	1971 I 143	BSP
<i>Mionictis</i>	FAM 49154	AMNH
<i>Mionictis</i>	FAM 50623	AMNH
<i>Mionictis</i>	FAM 144550	AMNH
<i>Mionictis</i>	FAM 27429	AMNH
<i>Mionictis</i>	FAM63296	AMNH
<i>Mionictis</i>	347-1079	AMNH
<i>Mionictis pristinus</i>	FM 10811	AMNH
<i>Mirounga angustirostris</i>	USNM 265353	USNM
<i>Mirounga angustirostris</i>	USNM 484893	USNM
<i>Mirounga angustirostris</i>	USNM 21895	USNM
<i>Mirounga angustirostris</i>	USNM 260867	USNM
<i>Mirounga angustirostris</i>	USNM 21890	USNM
<i>Mirounga angustirostris</i>	USNM 12441	USNM

<i>Mirounga angustirostris</i>	USNM 239141	USNM
<i>Monachus monachus</i>	USNM 243842	USNM
<i>Mustelavus priscus</i>	YPM 13775	YPM
<i>Mustelavus priscus</i>	YPM 13776	YPM
<i>Mustelavus priscus</i>	YPM 13777	YPM
<i>Mustelid indet</i>	P14935	FM
<i>Mydaus javanensis</i>	USNM 156287	USNM
<i>Mydaus marchei</i>	USNM 478276	USNM
<i>Neotherium mirum</i>	PAL 11542	USNM
<i>Neotherium mirum</i>	USNM 11548	USNM
<i>Neovison vison</i>	NMC 41100	CMN
<i>Neovison vison</i>	NMC 75540	CMN
<i>Neovison vison</i>	NMC 55365	CMN
<i>Oligobunis</i>	JODA 4332	JODA
<i>Oligobunis darbyi</i>	YPM 10272	YPM
<i>Otaria</i>	USNM	484912
<i>Pagophilus groenlandica</i>	75421	CMN
<i>Pagophilus groenlandica</i>	75363	CMN
<i>Pagophilus groenlandica</i>	75364	CMN
<i>Paradaphoenus cuspidatus</i>	AMNH 6853	JODA
<i>Paragale hurzeleri</i>	PH 3638	NHMB
<i>Paragale hurzeleri</i>	MA 4641	NHMB
<i>Paragale hurzeleri</i>	SG 3214	MNHN
<i>Paroligobunis frazieri</i>	USNM 460297	USNM
<i>Phoca groenlandica</i>	ROM 91303	ROM
<i>Phoca vitulina</i>	75385	CMN
<i>Phoca vitulina</i>	5373	CMN
<i>Phoca vitulina</i>	USNM 550330	USNM
<i>Pinnarctidon</i>	USNM 314325	USNM
<i>Piscophoca</i>	SAS 564	MNHN
<i>Piscophoca</i>	SAS 72	MNHN
<i>Piscophoca</i>	SAS 682	MNHN
<i>Piscophoca</i>	SAS 488	MNHN
<i>Piscophoca</i>	AMNH 125629	AMNH
<i>Plesictis branssatensis</i>	97448	FSL
<i>Plesictis branssatensis</i>	97708	FSL
<i>Plesictis branssatensis</i>	97709	FSL
<i>Plesictis curvatus</i>	BSP 1976 XVII 3420	BSP

<i>Plesictis genetoides</i>	FAM 11001	AMNH
<i>Plesictis genetoides</i>	COD2181	NHMB
<i>Plesictis julieni</i>	97,710	FSL
<i>Plesictis julieni</i>	SG 3209a	MNHN
<i>Plesictis julieni</i>	SG3210	MNHN
<i>Plesictis palmidens</i>	FAM 10090	AMNH
<i>Plesictis palmidens</i>	1879 XV 75	BSP
<i>Plesictis palmidens</i>	1879 XV 718	BSP
<i>Plesictis palmidens</i>	1875 XV 713	BSP
<i>Plesictis palmidens</i>	????	BSP
<i>Plesictis palustris</i>	SG 1897 17	MNHN
<i>Plesictis pygmaeus</i>	YPM PU 11571	
<i>Plesictis pygmaeus</i>	42043	MGL
<i>Plesictis robustus</i>	SG 3213	MNHN
<i>Plesictis sp.</i>	BST 3853	NHMB
<i>Plesictis sp.</i>	SG 11982	NHMB
<i>Plesictis vireti</i>	1937 II 13212	BSP
<i>Plesictis vireti</i>	1937 II 13226	BSP
<i>Plesictis vireti</i>	1937 II 13382	BSP
<i>Plesiogale angustifrans</i>	SG 28941	NHMB
<i>Plesiogale angustifrans</i>	SG 3192/3193	MNHN
<i>Pontolis</i>	USNM 335567	USNM
<i>Potamotherium</i>	FAM 49424	AMNH
<i>Potamotherium</i>	SG4367	NHMB
<i>potamotherium</i>	SG7624	NHMB
<i>potamotherium</i>	SG7626	NHMB
<i>Potamotherium</i>	SG7622	NHMB
<i>Potamotherium</i>	SG 15087	NHMB
<i>Potamotherium</i>	SG 15088	NHMB
<i>Potamotherium</i>	SG7628	NHMB
<i>Potamotherium</i>	SG7627	NHMB
<i>Potamotherium</i>	SG15084	NHMB
<i>Potamotherium</i>	SG4405	NHMB
<i>Potamotherium</i>	SG4408	NHMB
<i>Potamotherium</i>	SG4414	NHMB
<i>Potamotherium</i>	SG4415	NHMB
<i>Potamotherium</i>	SG6987	NHMB
<i>Potamotherium</i>	SG6988	NHMB

<i>Potamotherium</i>	SG12352	NHMB
<i>Potamotherium</i>	SG20078	NHMB
<i>Potamotherium</i>	SG20080	NHMB
<i>Potamotherium</i>	SG20076	NHMB
<i>Potamotherium</i>	SG17987	NHMB
<i>Potamotherium</i>	SG8012	NHMB
<i>Potamotherium</i>	SG 8006-12	NHMB
<i>Potamotherium miocenicum</i>	1964 I 225	BSP
<i>Potamotherium miocenicum</i>	????	BSP
<i>Potamotherium valetoni</i>	AMNH 10085	AMNH
<i>Potamotherium valetoni</i>	SG836	NHMB
<i>Potamotherium valetoni</i>	SG 229	NHMB
<i>Potamotherium valetoni</i>	SG 226	NHMB
<i>Potamotherium valetoni</i>	213902	FSL
<i>Potamotherium valetoni</i>	1885 I 13	BSP
<i>Potamotherium valetoni</i>	1971 I 147	BSP
<i>Potamotherium valetoni</i>	SG 692	MNHN
<i>Potos flavus</i>	ROM 37322	ROM
<i>Procyon Lotor</i>	FAM 1435? Teaching collection	AMNH
<i>Promartes lepidas</i>	P12155	FM
<i>Promeles</i>	PIK-3454b or M9030	MNHN
<i>Promeles</i>	PIK-3454b or M9029	MNHN
<i>Promeles</i>	PIK-3454a	MNHN
<i>Promephitis lartetii</i>	PIK-3019 a and b	MNHN
<i>Proneotherium repenningi</i>	USNM 335526	USNM
<i>Proneotherium repenningi</i>	USNM 206275	USNM
<i>Proneotherium sp</i>	USNM 3355526	USNM
<i>Pseudobassaris riggsi</i>	YPM PU 11455	YPM
<i>Pteronarctos goedertae</i>	USNM 335432	USNM
<i>Pteronarctos goedertae</i>	USNM 167648	USNM
<i>Pteronarctos goedertae</i>	VP 88930	UWBM
<i>Satherium</i>	FAM 87403	AMNH
<i>Semantor macrurus</i>	AMNH 100013	AMNH
<i>Simocyon primigenius</i>	JODA 101718 Cast of YPM 10043	JODA
<i>Simocyon primigenius</i>	YPM PU 11649	YPM
<i>Simocyon primigenius</i>	AS II 51	BSP
<i>Simocyon primigenius</i>	AS II 52	BSP

<i>Simocyon primigenius</i>	PIK-3277	MNHN
<i>Simocyon primigenius</i>	PIK-3274	MNHN
<i>Simocyon primigenius</i>	PIK-3299	MNHN
<i>Sthenictis</i>	FAM 25235	AMNH
<i>Stromeriella franconica</i>	10356	BSP
<i>Stromeriella franconica</i>	1976 xxii 3494	BSP
<i>Stromeriella franconica</i>	1937 II 13533	BSP
<i>Stromeriella franconica</i>	1937 II 13535	BSP
<i>Stromeriella franconica</i>	1971 I 150	BSP
<i>Stromeriella franconica</i>	1937 II 13534	BSP
<i>Stromeriella franconica</i>	1937 II 13540	BSP
<i>Stromeriella franconica</i>	1937 II 13606	BSP
<i>Stromeriella franconica</i>	1937 II 13561	BSP
<i>Taxidea taxis</i>	JD-0-121	JODA
<i>Taxidea taxis</i>	NMC 5350	CMN
<i>Taxidea taxis</i>	NMC 75351	CMN
<i>Taxidea taxis</i>	NMC 44056	CMN
<i>Taxidea taxis</i>	NMC 44031	CMN
<i>Taxidea taxus</i>	1971 I 138	BSP
<i>Thalassoleon macnallyae</i>	AMNH 144645	AMNH
<i>Thalassoleon macnallyae</i>	USNM 263570	USNM
<i>Thalassoleon macnallyae</i>	USNM 184076	USNM
<i>Thalassoleon mexicanus</i>	Cast of IGCU 902 (USNM 215020	USNM
<i>Ursavus</i>	JODA 2396	JODA

Appendix C: Characters used in phylogenetic analysis

Skull

1. Temporal lines (Wang et al, 2005: character 1)

0=converge to form a sagittal crest,

1=parallel, do not form a sagittal crest.

The derived character state, in which the temporal crests never communicate with each other, appears to have arisen independently at least three times in arctoids: in phocids, in *Plesictis*, and in the leptarctines. The leptarctines and *Plesictis* display widely separated temporal lines.

2. Frontal, anterior root of sagittal crest (Boessenecker and Churchill, 2015; character 34)

0=crest emerges from one point of supraorbital process, either from one point or slightly bifid

1=anterior emergence of crest bifid, and preceded by prominent divergent crests that originate on the posterior portion of the supraorbital process

3. Postorbital constriction (modified from Wolsan, 1993: character 1; Wang et al, 2005: character 34).

0= short

1=intermediately long

2=long

Postorbital constriction is considered long when it is longer than its greatest width. Post-orbital constriction refers to the constriction of the skull in ventral view immediately posterior to the orbits. Here, the distance is measured from the supraorbital processes to the postorbital constriction itself (that is where this region is most narrow), prior to the posterior expansion of the skull caused by the braincase. Post-orbital constriction is likely a synapomorphy of pinnipedimorphs, but also occurs in the early-diverging Amphicyonid, *Temnocyon*.

4. Palatine, anterior palatine foramina {1} <15> (Berta, 1991: character 5; Bryant et al., 1993: character 1)

0=located at maxilla/palatine suture

1=anterior to the suture

The plesiomorphic condition, anterior palatine foramina located at the maxillary-palatine suture, occurs in canids, ursids, Amphicyonids, ailurids, Phocines, and non-aquatic mustelids. Anteriorly-located foramina arise appear to arise independently in pinnipedimorphs, mephitids, and aquatic mustelids, excepting the aberrant mid-Miocene *Mionictis*.

5. Palatine, posterior limit (Wang et al., 2005; character 2)

0=located near the posterior limit of the toothrow,

1=expanded, posterior to toothrow

In Amphicyonids, canids, and some early-diverging musteloids, the palatine does not extend significantly beyond the toothrow. In *Puijila*, *Potamotherium* and many derived musteloids the posterior choana opens near the level of the glenoid fossa.

6. Palatine, width of posterior margin (modified from Wyss and Flynn, 1993; Wozencraft, 1989)

0=nearly equal to intercanine width

1=somewhat wider than width between canines; >1.1x wider

2=significantly wider than width between canines >1.5x wider

monachine seals display a highly divergent tooth row, with the width at the posterior margin over three times as wide as the width at the canines. Divergent tooth rows (>1.5x wider than width at canines) are also observed in canids, phocids, and desmatophocines, among other taxa. Wyss and Flynn (1993) suggested this likely represents a phocoid (Phocidae + Desmatophocidae) synapomorphy. However early-diverging odobenids, including *Proneotherium* and *Prototaria*, display tooth rows that are no less divergent than those of *Desmatophoca*.

7. Palatal midline ridge (Rybczynski et al., 2009; character 4)

0=absent

1=present.

The appearance of the palatal midline ridge is highly variable, with the most common condition consisting of a mediolaterally-thick anterior ridge fading into a thinner posterior ridge, as observed in *Puijila*, *Potamotherium*, *Kolponomos*, *Allocyon*, *Amphicticeps* and *Desmatophoca brachycephalus*. This trait is likely a synapomorphy of pinnipedimorphs and their ancestors. This configuration is best exemplified by *Puijila* and *Amphicticeps*. The ridge, when present is highly variable in form. A less sharply-defined ridge is present in *Pteronarctos*, *Imagotaria*, and *Allodesmus*.

8. Palate, arching (Deméré and Berta, 2001: Character 6)

0=relatively flat

1=transversely arched (palatal arch averages >30)

A transversely arched palate has been identified as an odobenid synapomorphy (Kohno, 2006; Boessenecker and Churchill, 2013), but also appears in a number of aberrant pinnipedimorphs. Deméré and Berta (2002) polarized this trait by developing a 'Palatal-arch ratio' to quantify the character. As many of the fossils studied preserve this area poorly, we do not follow their convention of computing an average palatal arch-ratio, but instead take the relevant measurements (ratio of palatal midline depth to chord length of transverse arch) at the transverse plane of the lingual border of the P4.

9. Palatine, incisive foramina (modified from Valenciano et al., 2016: character 3)

0=located at the level of C

1=located at the level of C-I3 diastema

2=elongated; continue well posteriorly to C

3=absent

In many arctoids, the incisive foramina (their ventral opening) are aligned with the canine (state 0), or located slightly anteriorly to it, occasionally due to an extended C-I3

diastema (state 1). In state 2, observed in some phocids and some early pinnipeds, the incisive foramina are located well posteriorly of the canine. Most specimens of *Odobenus* completely lack incisive foramina.

10. Maxilla, palatine process (=pterygoid process) (modified from Berta, 1991: character 1)

0=absent

1=posterolaterally-directed point

2=thin and broad shelf

Our coding of this process reflects the description of Berta (1991). In the plesiomorphic condition, the palate, posterior to the molars, narrows quickly after the tooth row, becoming as narrow as the pterygoids. In this condition, the lateral margin of the posterior most portion of the palate is straight or concave. In ursids and some pinnipedimorphs, the posterior portion of the palate is laterally expanded, and a spur of bone projects posteriorly. No mustelids display development of this process, but specimens of *Mydaus* and *Conepatus* display incipient development of this process. phocids may atavistically retain this process, as it is present in some specimen of *Lobodon*, and is present in *Erignathus*. In some other pinnipedimorphs, the lateral margin may be expanded as a thin broad shelf, that comes to a cornered edge posterolaterally

11. Embrasure pit between P4/ M¹ (Berta, 1991: character 34)

0=present and deep

1=shallow or absent

12. Maxilla, nasolabialis fossa (modified from Berta, 1991; character 2)

0=absent or very weakly developed

1=present

The nasolabialis fossa is a variably-deep depression located immediately anteromedially to the anterior orbital rim, which serves to house the levator (=quadrator) labii superioris muscle, which is involved with retraction of the upper lip. The nasolabialis fossa is absent in canids, but its presence may be plesiomorphic for arctoids, appearing in Cephalogale, Allocyon and Amphicticeps, three taxa near the base of Arctoidea. It is also absent in derived ursids, mephitids, procyonids, and crown pinnipeds.

13. Maxilla, fossa muscularis (Berta, 1991 : character 32)

0=absent

1=present

The fossa muscularis is located within the anterior orbital margin, dorsomedial to the infraorbital foramen, and serves as the origin for the interior oblique muscle of the eye (Davies, 1964). A somewhat deeper pit, nearly resembling a foramen is present in ursids and some derived mustelids. A shallow depression that does not pierce the lacrimal bone is observed in stem pinnipeds and cephalogale.

14. Maxilla, contribution to orbital wall (modified from Berta and Wyss, 1994: character 9)

0=no contribution

1=small contribution; just a sliver of maxilla squeezes onto orbit
2=contributes heavily to anteromedial wall of orbit
3=contributes heavily to anteroventral wall of orbit, and slightly wraps over the orbital rim

15. Infraorbital foramen, in anterior view (modified from Berta and Wyss, 1994: character 11)

- 0=slit-like with long canal
- 1=rounded with long canal
- 2=rounded with short canal (canal does not extend past foramen)
- 3=rounded and large (mediolaterally wider than max length of incisive foramina in ventral view)

A slit-like infraorbital opening leading to a long canal is the plesiomorphic conditions for caniformes, and is observed in canids, Amphicyonids, and some ursids. A round infraorbital foramen appears in all other arctoids, though its size and the length of the canal vary considerably. Some mustelids have longer canals, but most have short canals, and moderately-sized foramina. pinnipeds and their ancestors, and other aquatic arctoids (including otters and *Mionictis*) display a large, round infraorbital foramen with a short canal.

16. Caninus fossa (=infraorbital fossa) (Bininda-Emonds and Russell, 1996; character 19)

- 0=absent; portion of maxilla lateral to tooth row is convex
- 1=present; portion of maxilla lateral to tooth row is concave

If present, the caninus fossa appears anteriorly on the alveolar margin of the maxilla. It is unknown if the phocid caninus fossa accommodates the nasolabialis muscle or the caninus muscle ((de Muizon, 1982), or whether the two muscles are even distinct from each other or synonymous (Bininda-Emonds and Russell, 1996). The caninus fossa was used as a synapomorphy of Phocines by de muizon (1982a), but appears more broadly throughout pinnipedimorphs. However, it does appear more prominent in many phocids (excepting *Erignathus*) than in non-phocids.

17. Orbital Vacuities (modified from Kohno, 2006: character 20)

- 0=absent
- 1=present, anteriorly positioned
- 2=present, posteriorly positioned
- 3=present, anteriorly positioned with dorsal portion eclipsing frontal or orbitosphenoid

The orbital vacuity (=sphenopalatine vacuity) is enlarged in all pinnipeds compared to terrestrial carnivorans. However, the make-up of this vacuity differs between the three families. In otariids the vacuity is greater and eclipses the bone dorsad of it (state 3). This condition is approached by monachines, but the eclipse of the bone dorsad to it (either the frontal or the orbitosphenoid) is not observed to the same extent. In Phocines, the vacuity is smaller and does not contact the frontal or orbitosphenoid

18. Nasals, in dorsal view

- 0=most posterior point occurs at midline; taper posteriorly
- 1=posterior margin is rounded; taper posteriorly
- 2=posterior margin forms an “M” shape; lateral margin straight and parasagittal or anterior portion tapers posteriorly, and posterior portion is straight or appears somewhat divergent
- 3=straight, transverse posterior margin; lateral margin straight and parasagittal

In state 2, exhibited by otariids, the anterior portion of the nasals may taper strongly posteriorly, as in *Arctocephalus*, and the posterior portion may appear slightly divergent, rather than parasagittally straight. Nevertheless, the key distinction is the shape of the posterior margin.

19. Anterior Narial opening (Kohno, 2006: character 2)

- 0=large, thin margin, and rounded
- 1=large thick margin and dorsoventrally elliptical
- 2=large thick margin with prenarial shelf

20. Premaxilla-nasal contact, in dorsal view (modified from Wyss and Flynn, 1993; character 5)

- 0=40-60% of length of nasal, no contact with frontal
- 1=less than 40% length of nasal, no contact with frontal
- 2=more than 60% length of nasal, no contact with frontal
- 3=more than 60% length of nasal, contacts frontal

The length of the contact between the premaxilla and nasal is substantial in many caniforms. A short nasal process of the premaxilla has been reported as a possible synapomorphy of phocoids (Wyss and Flynn, 1993; Berta and Wyss, 1994). However, a shortened contact between the premaxilla and nasal bones occurs in a variety of fossil taxa, including *Potamotherium*, which displays shortened nasals and *Amphicticeps*, which displays elongated nasals. Additionally, adult male specimens of *Arctocephalus* display a premaxilla-nasal contact that is no less shortened than that examined in several genera of phocids (e.g., *Phoca*, *Halichoerus*).

21. Antorbital process (modified from Deméré, 1994b)

- 0=absent or small
- 1=present on maxilla/frontal suture
- 2=present on maxilla
- 3=present on frontal

The plesiomorphic condition is a small antorbital process, represented by either a small bump or a vertically-elongated and slightly-protruding extension of the frontal and/or the maxilla. Odobenids and otariids display larger antorbital processes, though the placement of these processes slightly differs. Some other arctoids, like *Potamotherium*, and *Enhydra*, occasionally display small, but conspicuous antorbital processes that project well into the orbit.

22. Lacrimal

- 0=present, contact maxilla only,
- 1=present, contacts maxilla and jugal

2=absent

3=foramen present, but sutures in adult are fused

The lacrimal is large in most arctoids, but is lost in pinnipeds. It is difficult to code this character for many pinnipedimorphs, and some other musteloids, as the lacrimal become well-fused to the surrounding bones throughout ontogeny, obscuring the extent of the lacrimal and even its presence. In otariids, the lacrimal is present at an early age, but fuses to the maxilla and frontal (not the jugal) (King, 1971; Berta and Wyss, 1994). Wozencraft (1989) noted the presence of a vestigial lacrimal foramen in otariids, and Bininda-Emonds and Russell (1996) observed a similar vestigial foramen in *Odobenus*.

23. Zygomatic arch

0=horizontally flat,

1=slightly dorsally arched

2=strongly dorsally arched, steeply inclined from the glenoid.

The zygomatic arch is plesiomorphically only slightly dorsally arched. In some pinnipeds, it becomes horizontally flat or ventrally arched anteriorly. Measurements are taken from the most dorsal point of the glenoid to the most dorsal point of the zygomatic arch, not including the jugal process. Skull height is taken from the most dorsal point of the glenoid to a point along the dorsal edge of the skull that is aligned to the coronal plane.

24. Posterior portion of zygoma in dorsal view (Churchill and Boessenecker, 2014: character 38)

0=straight or somewhat medially bowed

1=deflected laterally

25. Zygomatic arch, jugal-maxillary contact in ventral view

0=interlocking

1=overlapping.

In state 1 (overlapping), the maxilla is medial to the jugal. In state 0, the most posterior process of the maxilla occupies a portion between the upper and lower processes of the jugal, appearing arrow-like.

26. Zygomatic arch, jugal-squamosal contact in lateral view (modified from Kohno, 2006: character 19)

0=overlapping, anterior end of squamosal immediately posterior to postorbital process of the jugal

1=interlocking

2=overlapping, with anterior end of squamosal located well posterior to the postorbital process of the jugal.

3=thin and shortened

For state 1 (interlocking) the jugal-squamosal contact forms a V-shape that points anteriorly, exemplified by *Allodesmus* or *Desmatophoca*. For state 2, the anterior end of the squamosal, where it overlies the jugal, is thinner than the jugal. For state 3, the jugal and squamosal are only weakly fused, even in adult odobenines, representing a synapomorphy for the clade.

27. Frontal, supraorbital process (modified from Berta 1991: character 7))

0=small, not projecting

1=absent

2=large, forming a shelf-like, quadrate, lateral projection

3= extensive; temporal crests continue into laterally projecting process that comes to a point

Situated at the dorsal-most portion of the interior margin of the orbit, the supraorbital processes are plesiomorphically thin and laterally-projecting in canids (state 3), but become reduced and do not project laterally in stem arctoids (state 0). odobenids and phocids display a complete lack of supraorbital processes, while otariids display large, anteroposteriorly widened supraorbital processes that also project significantly laterally. This trait may be correlated with size of the frontal sinuses, which often are housed by or incompletely protrude into the supraorbital processes.

28. Optic Foramina, visibility through skull in lateral view (modified from Furbish, 2015: character, 20)

0=do not pierce skull, or produce a slight opening not immediately visible in lateral view

1=pierce skull in the form of a large, immediately visible opening

State 0 is typical for carnivorans, in which optical foramina are present on the lateral surface of the postorbital region, opening into obliquely angled optic canals. In some arctoids, the optic foramina may be just barely visible on the other side of the skull if the skull is oriented in a very specific manner. We do not code this condition as derived. Alternatively, in state 1, characterizing later diverging otariids, the optical foramina contact each other, and this confluence produces a common fissure visible on both sides of the skull.

29. Alisphenoid canal, foramen rotundum

0=located within alisphenoid canal, separated from orbital fissure

1=located within alisphenoid canal; alisphenoid shares common opening with orbital fissure

2=separate individual opening; separated from alisphenoid canal (if present) and orbital fissure/anterior lacerate foramen

3=shares a common opening with orbital fissure

30. Alisphenoid canal, caudal (alar) opening (modified from Wolsan, 1993: character 4)

0= present

1= absent

In many mammals the alisphenoid canal (alar canal) opens posteriorly forming the caudal alar opening located near the foramen ovale. The alisphenoid canal is independently lost in mustelids (not including paleo-mustelids/oligobunines) and phocids, with possible independent losses occurring in *Potamotherium*, and possibly *Mionictis*. Other pinnipeds typically display a shortened alisphenoid canal. One specimen of *Callorhinus ursinus*

(ROM 94.1.8.3 (Mam. 31E.1.2)) lacks an alisphenoid canal on its left side, leaving behind only a shallow groove (there is no sign of breakage on this specimen).

31. Alisphenoid, pteryoid strut bracing posterior part of palate against braincase (Kohno 2006: character 13)

- 0=slender
- 1=dorsoventrally thin and laterally projected
- 2=dorsoventrally thick and laterally broad
- 3=laterally thin and rolled

32. Parietal-squamosal contact (Furbish, 2015: character 13)

- 0=straight
- 1=parabolic

33. Squamosal, postglenoid foramen (Wyss and Flynn, 1993)

- 0=present and large
- 1=vestigial or absent

The post-glenoid foramen connects the external jugular vein and the superior venous sinus (Wyss and Flynn, 1993). Most arctoids have a large postglenoid foramen, posteriorly appressing the glenoid fossa. The post-glenoid foramen is completely absent in pinnipeds, and reduced in their fossil relatives, including *Enaliarctos* and *Puijila*. Tedford (1994) suggests the loss of the post-glenoid foramen may be an adaptation for internal jugular drainage, and thus may be convergent in these taxa.

34. Glenoid fossa (Kohno 2006: character 26)

- 0=deep
- 1=shallow and anteroposteriorly broad
- 2=laterally-shortened

35. Anteroventrolateral corner of braincase (modified from Mitchell and Tedford, 1973; Churchill and Boessenecker, 2014: character 49)

- 0=smoothly rounded
- 1=square; nearly forms a right angle

36. Squamosal, pseudosylvian sulcus on braincase (Berta, 1991: character 17)

- 0=weakly present or absent
- 1=prominent

The pseudosylvian fissure is formed in the anterior half of the brain and is oriented vertically, or slightly caudally. In some taxa the fissure is very deep and results in the formation of a corresponding groove that can be seen on the outside of the braincase. Many fossil pinnipeds, including *Potamotherium*, the Enaliarctines and the DesmatoPhocines, display a prominent pseudosylvian sulcus, while many later-diverging pinnipeds lack this feature, or exhibit a reduced condition, including *Acrophoca* and *Imagotaria*. To our knowledge, a prominent pseudosylvian sulcus has not been reported in fully mature specimens of any extant pinnipeds. However, all adult male specimens of *Arctocephalus* possess a prominent indentation in the position of the pseudosylvian

sulcus. Furthermore, juvenile individuals of other crown otariid genera (e.g., *Callorhinus*) may also display a prominent pseudosylvian sulcus. Some other musteloids, including *Ailruus* and *Sthenictis* display a very weakly defined pseudosylvian sulcus.

37. Postlateral sulcus aka entolateral sulcus (Wolsan, character 11)

- 0=absent
- 1=present

38. Cruciate sulcus (Radinsky, 1971)

- 0=large or unreduced
- 1=absent or very reduced

39. Postsylvian sulcus (Bryant et al., 1993: character 37)

- 0=long; vertically oriented
- 1=short; no ventral extension

40. Coronal Gyrus

- 0=narrow
- 1=expanded; wide

The coronal gyrus, enclosed anteriorly by the coronal sulcus and posteriorly by the suprasylvian sulcus, roughly corresponds to the primary somatosensory cortex (Radinsky, 1968; Sawyer et al., 2016) and is anteroposteriorly broadened (state 1) in some semi-aquatic taxa (excepting *Enhydra*). Some pinnipedimorphs display an intense broadening of this area. Extant pinnipeds typically display a coronal gyrus that is less obliquely-oriented, and less broadened than that of pinnipedimorphs but still large relative to that of terrestrial carnivorans (personal obs.). The somatosensory cortex in pinnipeds is not as strictly circumscribed by the coronal sulcus, explaining the partial reduction in coronal gyrus size. In state 0, the coronal gyrus is not particularly enlarged compared to the other gyri of the brain.

41. Squamosal, mastoid process (modified from Berta and Wyss (1994): characters 23 and 24)

- 0=not prominent
- 1=laterally projecting with a curving ventral extension; anteroposteriorly constricted
- 2=laterally projecting, anteroposteriorly constricted with a concave posterior face
- 3=laterally projecting and dorsoventrally constricted/bulbous
- 4=pachyostotic

The extent of the mastoid process may not be completely independent of the extent of the mastoid sinus. Thus, our character states for the mastoid depend on the extension beyond the endocranial swellings. In state 2, the posterior surface of the mastoid process may be strongly concave (as in *Puijila*), or weakly concave (as in *Enaliarctos emlongi*).

42. Squamosal, Paroccipital process

- 0=small with no discernable shape
- 1= enlarged and excavated

- 2= enlarged and unexcavated
- 3=rod-like; much longer than wide
- 4=flattened and wider than long
- 5= mediolaterally compressed; comes to a point ventrally enlarged and excavated

The paroccipital process serves as the origin of the digastric muscle, which is the sole muscle used to open the jaw (Ewer, 1973). A discrepant distribution of the various states across caniformes suggests the size and shape of the paroccipital process are highly homoplastic. The relationship between the paroccipital and the mastoid appears to have phylogenetic significance in arctoids (Berta and Wyss, 1994).

43. Relationship between paroccipital and mastoid processes (modified from Berta and Wyss (1994): character 24)

- 0=not closely associated or connected by a low (dorsally high) ridge
- 1=connected by a high crest

44. Squamosal, suprameatal fossa (Wang et al, 2005: character 5)

- 0=absent or a mere depression,
- 1=small dorsal excavation
- 2=dorsally deep
- 3=partially covered anteriorly

The suprimeatal fossa is a concavity formed on the cranial surface of the external auditory meatus. A small suprimeatal fossa arises independently multiple times, becoming enlarged in some musteloids (Wang, et al., 2005), and appearing partially closed by posterior wall of meatus, as seen in some musteloids including mustelines (weasels) and lutrines (otters) among others (Wolsan, 1993).

45. Squamosal, epitympanic recess and epitympanic sinus (modified from Wolsan, 1993: character 9 Decker and Wozencraft, 1993; Bryant et al., 1993: character 34; Ahrens, 2012: characters 23 and 24)

- 0=absent
- 1=present but unexpanded
- 2=expansion into mastoid and squamosal areas to produce a large accessory chamber
- 3=very deep (dorsally excavated) epitympanic recess, reaching above promontory, and mediolaterally wider than carotid canal
- 4=epitympanic recess not expanded, but middle ear cavity invades mastoid region via posterior expansion

The epitympanic sinus is an accessory cavity of the tympanic cavity located lateral and somewhat dorsal to the epitympanic recess, to which it opens into. Possession of an epitympanic sinus (state 1) was previously considered a synapomorphy of Procyonidae, but inspection of XRHCT data has challenged this interpretation (Ahrens, 2012). Ahrens defined the epitympanic sinus as a dorsal expansion of the epitympanic recess. We prefer Segall's (1943) and Whitmore's (1953) definition, though we agree with Ahrens (2012) that possession of the epitympanic sinus is more broadly distributed than previously believed. Nevertheless, the Procyonidae may display a unique state, in which the the

epitympanic sinus continues posteriorly as a canal that does not open into the tympanic cavity. *Canis* and *Melogale* display a similar condition, but their ‘canal’ abruptly ends nearly as soon as it becomes ventrally encompassed by temporal bone, while the canals of *Procyon* and *Potos* are further elongated, and are at least incipiently separated from the epitympanic recess. State 2, an extreme expansion of the epitympanic recess into the mastoid and squamosal, is a synapomorphy of mephitids (Wang et al., 2005), with at least one mephitid ancestor displaying a dorsally excavated epitympanic recess that does not penetrate the tympanic bone, possibly a transitional stage toward a completely formed mastoid sinus. Some mustelids display a mastoid sinus which is similar in appearance to the mastoid sinus of mephitids, but has no connection with the epitympanic recess, and is thus unlikely to be homologous (Geraads and Spassov, 2016). A deeply excavated and significantly broadened epitympanic recess (State 3) occurs in phocids (excluding monachus) and desmatophocids.

NOTE: The suprameatal fossa of mustelids, which extends ventrally and is closed anteriorly by the wall of the meatus, appears in a similar area to the epitympanic sinus, but ostensibly shares a similarity in form to the suprameatal fossa, and is thus, hypothesised to be homologous with the suprameatal fossa rather than the epitympanic sinus.

46. Basioccipital (modified from Berta and Wyss, 1994: Character 42)

0=not broadened

1=broad between bullae

2=short; wide and broader posteriorly

In most carnivorans the basioccipital is long and narrow. In many arctoids this element is broadened in ventral view, whereas in pinnipeds such as odobenids and phocids, the basioccipital is broader still, and also widens posteriorly. For measurements compare width of BO anteriorly with width of BO posteriorly near carotid foramen

47. Caudal portion of Basioccipital, in ventral view

0=no keel/crest; no excavation or minor excavation restricted to lateral portions

1=median keel present; no or little excavation

2=median keel prominent and diverges anteriorly to produce a Y-shaped crest; no or little excavation

3=Y-shaped crest prominent and encases deep triangular excavations on either side of median keel

A flat basioccipital is observed in many mustelids and phocids. Excavation of the lateral portions of the basioccipital is present in many taxa, to accommodate the rectus capitis ventralis muscles. This excavation is variable in its depth, and may or may not be paired with a median keel, which may or may not diverge anteriorly into two oblique crests.

48. Basisphenoid, in ventral view (modified from Berta and Wyss, 1994: character 44)

0=concave

1=convex

49. Basioccipital, inferior petrosal sinus (modified from Tomiya and Tseng, 2016)

0=indistinct embayment on lateral wall of basioccipital

1=shallow embayment; sinus with well-defined medial margin, but not particularly large

2=deep basioccipital embayment; sinus is deep with both medial and lateral edges sharp and well defined

This character refers to the portion of the petrosal sinus that is medial to the petrosal.

This character is most reliably identified in coronal slices of the basioccipital from CT data, but can also be visible if an unobscured dorsal view of the basioccipital region is possible. In the Amphicyonid condition, the lateral border of the basioccipital is strongly excavated, in the region running alongside the petrosal and carotid canal, resulting in a deep embayment enclosed by strong dorsal and ventral arms. In most other caniformes, including mustelids, only a minor dorsolateral excavation is present, and the shallow embayment lacks prominent arms. In some caniformes, no excavation is present whatsoever.

50. Basioccipital, posterior lacerate foramen

0= small

1=large and round

2=large, transversely oval

3=anteroposteriorly elongate fissure

The posterior lacerate foramen allows for the passage of the glossopharyngeal, vagus, and spinal accessory nerves. In caniformes, this opening also accommodates the internal jugular vein, except in some mustelids, who display a separated jugular foramen.

51. Auditory bulla, carotid canal, posterior opening (Wang, 2005: character 4)

0=adjacent to posterior lacerate foramen

1=considerably anterior to posterior lacerate foramen

State 1 arises independently in phocids and many musteloids. *Monachus* displays state 0, indicating that state 1 arose independently in phocids and desmatophocids.

52. Auditory bulla, carotid canal, anterior opening

0=vertical

1=horizontal, visible only from bullar chamber

In an intact skull the carotid canal opens so that it is visible on the ventral surface of the skull (character state 1). In character state 2, the carotid artery reaches the braincase from within the bulla, and does not show any external opening.

53. Auditory bulla, tubular external auditory meatus (Wolsan, character 8)

0=no differentiation of meatal trough of ectotympanic

1=meatal trough less than 1/3rd length of bulla

2=meatal trough more than 1/3rd length of bulla

54. Auditory bulla, ectotympanic, pseudoseptae (Wang, 2005: character 37)

0=absent

1=present

55. Crista tympani

0=small diameter; strongly produced into tympanic cavity

1=large diameter; not strongly produced into tympanic cavity

The tympanic crest (=crista tympani; =crista tympanica) is a medial projection of the lateral portion of the tympanic bone into the tympanic cavity, ventral to the external auditory meatus. In state 0, the tympanic crest is dorsoventrally thin and flange-like, and extends significantly into the tympanic cavity. In state 1, the tympanic crest is large both anteroposteriorly and dorsoventrally, but does not project as a flange significantly into the tympanic cavity. Tedford (1976) used this trait to ally *Enaliarctos* with otarioids and *Potamotherium* with phocids.

56. Cerebellar (=subarcuate=floccular) fossa

0=broad and deep

1=filled in by bone

Anteriorly, the subarcuate fossa, or cerebellar fossa, which houses the paraflocculus, begins as a medial excavation of the dorsal portion of the petrosal. In state 0, the subarcuate fossa expands posteriorly and eventually becomes enclosed by the petrosal. This fossa is large in canids and Carnivoran ancestors (*Miacis*), and experiences a great deal of variability in arctoids. In state 1, the fossa is filled in by bone and is not readily discernible. The polarity of this trait was formerly used to support a closer relationship between otariids and odobenids, but was seemingly discarded in the pinniped literature after Wyss (1987) comprehensively mapped the polarity of this feature in arctoids, determining both states were widespread among arctoids and the trait was not phylogenetically informative.

57. Carotid canal in ventral view (modified from Churchill and Boessenecker, 2013; 43; Bininda-Emonds and Russell, 1996; character 82)

0=obscured by medially-inflated caudal entotympanic; smoothly integrated into bulla

1=caudal entotympanic not medially-inflated; carotid canal well visible in ventral view and not smoothly integrated into bulla

2=caudal entotympanic projects medially and overhangs carotid canal

58. Auditory bulla

0=flattened

1=inflated and rounded

2=greatly inflated

3=very small, covering only a sliver of the tympanic cavity; not well-ankylosed to rest of skull

In character state 2 the caudal entotympanic portion of the bulla is inflated to such a degree that in ventral view it overhangs the posterior lacerate foramen. In some cases the posterior lacerate foramen may be obscured. State 3 is displayed by *Temnocyon*, fossil of which rarely preserve an entotympanic (Hunt, 2011).

59. Auditory Bulla, Posterior projection

0=absent

1=present

The tympanic bulla displays a posterior projection that may also overhang the posterior lacerate foramen, however, this obscurity is not caused by great inflation of the caudal entotympanic. (Churchill and Boessenecker, 2014)

60. Auditory bulla, caudal entotympanic (Hunt, 1974)

0= Type B; entotympanic contributes significantly more than ectotympanic

1= Type A; entotympanic and ectotympanic contribute similarly to bulla

61. Tympanohyal depression (modified from Bininda-Emonds and Russell, 1996: character 111)

0=closely associated with stylomastoid foramen,

1=separated and located posterior and/or medial to stylomastoid foramen

2=separated and located anterolateral to stylomastoid foramen

The tympanohyal depression provides a surface of attachment for the tympanohyal cartilage that is the most proximal element of the hyoid apparatus. This depression varies in size and depth across arctoids but is typically positioned posterior and/or medial to the stylomastoid foramen, and posterolateral to the auditory bulla, and may share a common fossa with the stylomastoid foramen, which permits the facial canal an exit from the skull. In many musteloids, it is very closely associated with the stylomastoid foramen (state 0), whereas in others, it is separated by a bony flange or a process (state 1). In phocids, the tympanohyal depression is widely separated from the stylomastoid foramen, and uniquely located antero-lateral to it (state 2).

62. Petrosal in ventral view, visibility in posterior lacerate foramen (Berta and Wyss (1994), character 34)

0=not visible

1= visible

In most arctoids the petrosal in the intact skull is not visible on the ventral surface of the skull (state 0). In character state 1 the petrosal is readily visible, and forms the anterior rim of the posterior lacerate opening.

63. Petrosal, connection to surrounding elements (Wozencraft, 1989; Bininda-Emonds and Russell, 1996)

0=well-fused ventromedially with basioccipital and laterally with temporal bone

1=loosely attached to surrounding bones; sits atop basioccipital, rather than firmly affixed to it

Repenning (1972) noted the petrosal isolation of the petrosal in phocids. HR μ CT allows for this feature to be clearly distinguishable. In pinnipeds, the petrosal, or at least its anterior portion, never fully fuses to the basioccipital, or the temporal bone. In 'fissipeds', these bones appear fully fused.

64. Tentorium (modified from Bryant et al., 1993: character 14; Kohno, 2006: character 29)

0=far from petrosal

1=appressed to petrosal

2= reduced

3=absent

In state 0, the tentorium is large, and while it does not directly appress the petrosal, it may originate just lateral to it. In state 1, the tentorium begins as a thickened, medially projecting process located just anterior and dorsal to the lateral half of the petrosal's dorsal surface, so that it appears this portion of the tentorium is perched upon the petrosal. In state 2, the tentorium is reduced, and its ventral-most portions contact the basicranial region well posteriorly of the tympanic bullae, or in the case of *Canis*, contact the temporal bones laterally. In state 3, the tentorium is completely absent, as observed in mephitids.

65. Bony Falx (Nojima, 1990)

0=absent

1=present, vertical; arises at junction with tentorium or anterior to it

2=present, only posteriorly as skull narrows

66. Petrosal, internal auditory meatus (Wyss and Flynn, 1993)

0= single rounded opening,

1= two openings, conjoined

2= two foramina

The internal auditory meatus transmits cranial nerves VII, and VIII. In state 0, these nerves share a common opening, or are only incipiently separated internally (the separation is not readily visible) (Sanfelice and Drehmer, 2013). In state 1, the nerves display a bilobed opening, readily apparent on the surface of the petrosal. In state 2, observed in phocids, distinctly separate openings exist for each nerve. State 1 has previously been proposed as an odobenid synapomorphy. However, a similar degree of separation is occasionally observed in *Potamotherium*, *Enaliarctos*, and some crown otariids. It is unclear if this condition departs significantly from the plesiomorphic condition.

67. Petrosal, fossa for tensor tympani muscle (modified from Berta and Wyss, 1994: character 30)

0=present as a dorsomedially excavated pit

1=absent

2=shallow groove restricted to lateral portion of promontory

Plesiomorphically for arctoids, the tensor tympani inserts on a depression on the lateral promontory wall, just anterior to the oval window. The fossa for the tensor tympani is typically very dorsally deep, although it becomes shallow in some pinnipedimorphs. In later-diverging pinnipeds, the tensor tympani inserts on the wall of the Eustachian Canal. *Pteronarctos* displays a unique condition, in which a groove on the lateral promontory wall is present, but it is not accompanied by any dorsal excavation.

68. Petrosal, Posterior promontorium process (Wang et al, 2005: character 27)

0=absent

1=present.

69. Petrosal, fenestra cochleae (= round window) (Wozencraft, 1988: character 42; Berta and Wyss, 1994: character 33)

0=opens into middle ear

1=opens externally (External Cochlear Foramen of Burns and Fay, 1970; de Muizon 1982a)

70. Petrosal, fenestra cochleae (=round window) (Wozencraft, 1988: character 43; Wyss and Flynn, 1993: character 24)

0=approximately equal in size to oval window

1=larger than oval window

In pinnipeds, a cochlear fossula is present, which is a distinct recess in the auditory capsule housing the round window (variably present in *Potamotherium* according to Flynn, 1988). (see Wyss, 1987 for alternative view on state definitions and coding of *Potamotherium*)

71. Petrosal, basal whorl of cochlea (Wozencraft, 1988: character 44; Wyss and Flynn, 1993: character 28)

0=posterolateral orientation

1=transverse to skull

72. Petrosal, canal for cochlear aqueduct (Berta and Wyss, 1994: character 32)

0=pierces the petrosal

1=merged with the round window

73. Basal whorl of scala tympani (Berta and Wyss, 1994: character 27)

0=small

1=enlarged

The basal whorl of the scala tympani is enlarged in pinnipedimorphs, including *Enaliarctos*.

74. Petrosal, shape in dorsal view (Berta and Wyss, 1994: character 29)

0= flattened with pointed apex

1= inflated, rounded with apex not pointed

2= greatly expanded with rounded apex blunter in outline

The apex refers to the anterior portion of the petrosal. In dorsal view, the petrosal is typically flattened, with a sharply pointed apex anteriorly. In most pinnipeds, the petrosal becomes somewhat dorsally inflated, and loses the sharpness of its apex, though retaining the general triangular shape of terrestrial carnivorans. In most phocids, the petrosal is further expanded dorsally, covering the entirety of the ventral portion of the petrosal in dorsal view, and the apex becomes blunt and amorphous, losing its triangular shape.

75. Incus (=epitympanic recess) (Berta and Wyss, 1994: character 46)

0=small

1=moderately large

2= large

3=very large

A greatly enlarged incus occurs in desmatophocines and phocids. This trait appears independent of the presence of an epitympanic recess. Enlarged ossicular mass is likely an adaptation for underwater hearing (Nummela, 2008)

76. Malleus, muscular process (Berta and Wyss, 1994: character 47; Flynn et al., 1988: characters 21, 22)

0=present, large process

1=present, small bump

2= absent

The muscular process is large in most fissipeds. Its apex serves as the insertion for the fossa for the tensor tympani (Miller, 1979). However, a reduction of the muscular process is observed in ursids (Wyss, 1987), though the fossa for the tensor tympani still inserts in a similar location on the malleus (Ruf and Maier, 2010). Thus this character is likely independent of character __.

77. Malleus, processus gracilis and anterior lamina (Wyss 1987; Wyss and Flynn, 1993)

0=well developed

1=small or vestigial

Reduction of the processus gracilis and anterior lamina characterizes pinnipeds. Some codings from Segall (1943)

Mandible

78. Flange below mandibular angle (Berta and Wyss, 1994: character 52)

0=absent

1=present

This flange provides attachment for the digastric muscle. In arctoids, the ventral margin of the mandible is typically smoothly curving in a dorsal direction towards the angular process. However, in some pinnipeds, including many phocids, desmatophocids, and *Otaria*, the ventral margin of the mandible drops slightly ventrally posterior to the molars, and then curves rather abruptly dorsally beneath the mandibular angle. This area serves as the insertion site for the digastric muscle (see character __) (Mori, 1958; Ewer, 1973)

79. Ascending ramus modified from Wang et al., 2005: character 25)

0=projected dorsally

1=inclined posteriorly

2= inclined anteriorly

80. Genial Tuberosity (Boessenecker and Churchill 2013: character 37)

0=Weakly-developed; Deepest point of mandible positioned centrally/posteriorly

1=Strongly developed; Deepest point of mandible positioned anteriorly

The genial tuberosity is a ventral expansion of the mandibular symphysis, typically observed in lateral view, and best exemplified by *Kolponomos* and the desmatophocids.

81. Angular process in ventral view

- 0=aligned with rest of ventral margin of mandible
- 1=deflected laterally
- 2=deflected medially and/or canted mediolaterally; not significantly expanded
- 3=deflected medially; significantly expanded process

82. Mandible, anterior portion of symphyseal region (Boessenecker and Churchill 2015, character 38)

- 0=Smooth compact bone
- 1=Rugose, vascular bone

Dentition

83. Shape of Upper Incisor Row (Welsey-Hunt and Flynn, 2005)

- 0=straight
- 1=parabolic

84. I¹ (Wozencraft, 1988)

- 0=present
- 1=absent

85. I¹ and I², crown, transverse grooves (Wozencraft, 1988: character 58)

- 0=absent
- 1=present

In state 1, the transverse grooves are remarkably distinct, abruptly penetrating the posterior face (occlusal surface) of the incisor roughly midway up the crown.

86. I³, lingual cingulum ((Berta and Wyss, 1994: character 59)

- 0=present
- 1=absent

87. Canine, lateral groove

- 0=absent
- 1=present

This groove travels along the length of the lateral surface of the canine, gently curving to follow the long axis of the canine. They appear in ailurids and potosine procyonids (Wang, 1997; Wallace and Wang, 2004; supplementary)

88. P¹ (Wyss and Flynn, 1993: character 33)

- 0=present
- 1=absent

The P¹ is plesiomorphically present in arctoids. The P¹ is lost independently in neomustelids, *ailurus*, and in some hypercarnivorous arctoids, like the canid *Enhydrocyon* and the ailurid *Simocyon*.

89. P¹- P² lingual cingula (Kohno, 2006: character 45)

- 0=distinct but small

1=well-developed with cuspules
2=weak and bulbous

90. P², pseudoprotocone (Wyss and Flynn, 1993 : character 34)

0=small, fissiped-like, or absent
1=large, molarized with cingula

State 1 refers to a mesial-bucally expanded P2 that resembles the molars in size and complexity. This arises independently in *Ailrurus* and *Kolponomos*.

91. P³ protocone shelf expanded lingually

0= absent
1= present

State 1 refers to molarization seen in the P3 of some pinnipeds. In these cases the tooth roots may also be expanded in size. In some early arctoids, the P3 is somewhat lingually expanded, with partially bilobed posterior roots. However, these early arctoids lack development of the lingual portion of the crown, and are thus coded as possessing the plesiomorphic state.

92. P⁴, parastyle (4) Wyss and Flynn, 1993: character 35)

0=absent or vestigial
1=present

The parastyle of the P4 is lost in later-diverging mustelids, but is present in paleomustelids, neomustelids, procyonids and their ancestors, *Puijila* and *Mustelavus*. The basal condition for Arctoidea appears to be the absence of a well-developed parastyle. The parastyle appears to have arisen early within Mustelida, before being lost again in mustelids. The presence of this trait in *Puijila* may represent a retention of the basal condition or an independent acquisition.

94. P⁴, carnassial notch (Wozencraft, 1988: character 67)

0=present
1=absent
2=vestigial

A well-developed carnassial notch is the basal condition for arctoids, and caniformes more broadly. The carnassial notch is lost independently in crown pinnipeds and neomustelids.

95. P⁴, protocone (modified from Wang et al., 2005: characters 10 and 11)

0 = conical and anteriorly positioned relative to the paracone
1= conical and centrally or posteriorly positioned relative to the paracone
2= shelf like and posteriorly positioned, no hypoconal basin
3= shelf like and with hypoconal basin
4= shelf like and with hypocone
5=absent
6=conical and with hypocone
7=shelf-like and centrally positioned relative to protocone

In some carnivorans, including ursids and basal pinnipeds the protocone is

undifferentiated, forming a shelf (= “crescentic protocone” of Wolsan, 1993). In derived pinnipeds, including *Thalassoleon*, the protocone is completely absent (see also Berta and Wyss, 1994: character 63). (modified from Wang et al, 2005: character 33). Character states 0 and 1 are associated with the presence of a cingulum.

96. Premolar/Molar relative size (Wozencraft, 1988: character 76)

0=approximately equal in size

1=M considerably reduced

2=M enlarged

The basal condition is ostensibly premolars and molars of equal size. The extreme reduction of molars characterizes pinnipeds and their fossil ancestors, but is also observed convergently in *Enhydrocyon*. Molar enlargement occurs in ursoids, and in littoral taxa that use their molars to crush sea-shells (*Mionictis*, possibly *Kolponomos*). Molar reduction is thought to be associated with hypercarnivory in some carnivorans, including the clade containing felids and hyaenids (Wyss and Flynn, 1993). A reduction of the M¹ also characterizes several arctoids which are known to be or thought to have been hypercarnivorous, including *Gulo*, *Megalictis*, and the earliest-diverging pinnipedimorphs.

97. P⁴, rooting (Boessenecker and Churchill, 2015; character 71)

0=3-rooted

1=3-rooted but posterior root bilobed

2=2-rooted

3=1-rooted

98. M¹, hypocone (Wozencraft, 1988: character 74)

0=lingual cingulum well developed, but no cusp

1=absent

2=present

The presence of a distinct cusp (the hypocone) on the lingual border of the M¹ appears to be the plesiomorphic condition in arctoids, with the cusp being replaced by prominent cingulum in ursids, mustelids, procyonoids, and ailurids, and the cusp being completely lost in pinnipeds, early neomustelids (*Plesiogale/Paragale*), and possibly Amphicyonodontinae (*Kolponomos/Allocyon*)

99. M¹, metaconule (Flynn et al., 1988: character 27)

0=present, small

1=present, large

2=absent

A small metaconule (=cusplule between metacone and protocone) is the plesiomorphic condition for arctoids. A distinctly large metaconule characteries crown ursids (and *Kolponomos*) and ailurids. The metaconule is absent in early-diverging Amphicyonids, early-diverging ursoids, paleomustelids and their descendents, and pinnipeds.

100. M¹, paraconule (Tedford et al., 1994 : character 8)

0=absent or small

1=present and large

The paraconule is a small cusplule located between the paracone and the protocone, typically along the path of the preprotocrista.

101. M¹, metacone vs paracone (Wesley-Hunt and Flynn, 2005: character 48)

0=paracone>metacone

1=paracone < or equal to metacone

Coding was applied only to unworn or little worn cusps. Height was observed in lateral view.

102. M¹, protocone and metaconule, longitudinal crest (modified from Flynn et al., 1988: character 28)

0=present and oriented laterally,(45 degrees or more)

1=present and oriented posteriorly

2=absent

Also referred to as the postprotocrista (Wang et al, 2005: characters 23 and 29. A prominent postprotocrista is the basal condition for arctoids, and characterizes Ursidae, Amphicyonodontinae, and Amphicyonidae. A reduction of the postprotocrista occurs in mustelids. The postprotocrista was independently lost in pinnipeds and mustelids. *Leptarctus* has a vestigial postprotocrista, as does *Puijila*.

103. M¹, preprotocrista (modified from Finarelli, 2008: character 47))

0=present

1=absent

104. M¹, parastyle (Tedford et al., 1994: character 7)

0=present

1=present, large

2=absent

Absence of a parastyle may be the basal arctoid condition, and reappears several times within Arctoidea. A small parastyle characterizes musteloids, some canids and some Amphicyonids, and may alternatively represent the plesiomorphic condition. The derived condition is a bulkier parastylar wing that protrudes mesiobuccally and rises well above the level of the paracone or metacone. This condition may have arisen early within Arctoidea (*Mustelavus*) and retained in early-diverging mustelids (paleomustelids and leptarctines) and early-diverging pinnipeds.

105. M¹, constriction between paracone + metacone and protocone (Wozencraft, 1988: character 75; Wolsan, 1993: character 17)

0=absent

1=present

State 1 refers to the internal constriction or ‘pinching’ observed in some arctoids, namely the oligobunines (Wolsan character 17:c-d)

106. M¹, lingual vs buccal half (Wolsan character 17)

- 0=buccal half longer
- 1=equal
- 2=lingual half longer

107. M¹, rooting (Kohno, 2006: character 49)

- 0=3-rooted
- 1=2-rooted
- 2=1-rooted
- 3=M1 absent

In state 1, the posterior roots of the M1 may be bilobed.

108. M², size (Flynn et al., 1988: character 25)

- 0=present, nearly equal in size to M1 (more than 0.5x M1 size)
- 1=reduced (less than 0.5x M1 size)
- 2=absent
- 3=present, large (as large or larger than M1)

“Reduced” molars (state 1) are smaller in size than M1, and have one or two roots.

109. M² position (Tedford et al., 1994: character 24)

- 0=posterior or posterolateral to M1
- 1=posterolingual to M1

The M2 is considered posterolingual to the M1 when its buccal border is aligned with or located lingual to the linguo-buccal centre of the M1.

110. M², metaconule (Tedford et al., 1994: character 6)

- 0=small or not developed
- 1=developed
- 2=absent

111. M², Postprotocrista

- 0=Present
- 1=Absent

112. M², Hypocone (Finarelli, 2008: character 56)

- 0=absent
- 1=cingulum

The M2 hypocone is not strongly developed in any arctoid taxa examined, appearing as an elevated ridge of lingual cingulum, much like that observed on the M1 in many arctoid taxa. An M2 hypocone is retained in canids, ailurids, and ursids, and is likely plesiomorphic for musteloids. Independent losses may have occurred in mustelids and procyonids, as a probable fossil mustelid (*Brachypsalis*) and probable fossil procyonid (*Stromeriella*) retain a hypocone.

113. M³ (Wozencraft, 1988: character 79)

- 0=present
- 1=absent

114. I₁, presence (Wozencraft, 1988: character 5)

0=present

1=absent

All known pinnipeds, including early-diverging stem forms, like *Puijila* and *Enaliarctos*, display only two lower incisors. It is assumed the first incisor is lost, as nearly all arctoids display an I₁ that is smaller than the other incisors. However, the homology of this feature is difficult to establish without ontogenetic insights. *Kolponomos* lacks an I₁ alveolus, and has been coded as possessing the derived condition, a notion corroborated by CT data (Tseng et al., 2016).

115. c, posterior crista (Boessenecker and Churchill, 2013: character 57)

0=absent

1=present

116. Lower postcanines, roots

0=Double

1=Single

117. P₁ (Wyss and Flynn, 1992 : character 40)

0=present

1=absent

118. Premolars, size

0=increasing posteriorly

1= P₃= P₄

State 1 refers to the condition observed in otarioids, in which the P₃ and the P₄ are the same size. In all other arctoids, the P₄ is at least somewhat larger than the P₃.

119. P₃, accessory cusps

0=no accessory cusps present

1=paraconid, metaconid and hypoconid present

2=paraconid and hypoconid present; metaconid absent

3=metaconid and hypoconid present; paraconid absent

4=paraconid and metaconid present; hypoconid absent

5=paraconid present; hypoconid and metaconid absent

The protoconid, the primary cusp of the premolars, may be flanked mesially by the paraconid, and distally by the closely appressed metaconid and a hypoconid situated along the distal border. These cusps are completely lacking in extant mustelids, otariids, and ursids, but appear prominently in other arctoids. Several early pinnipedimorphs display all three cusps.

120. P₄, accessory cusps

0=no metaconid, distal wall of protoconid convex or flat

1=all

2=metaconid present, but lacking paraconid

3=metaconid absent; distal wall of protoconid concave

Similar to their P₃ accessory cusps, mustelids have reduced the prominence of the accessory cusps of their P₄, while many canids, pinnipeds, and procyonids display the full suite of accessory cusps.

121. M₁, Metaconid on ml (Wang et al, 2005: character 17).

0=equal or higher than paraconid

1=lower than paraconid

2=absent.

122. M₁, metaconid mesiodistal position

0=aligned with protoconid; well-defined wall

1=posteriorly displaced beyond protoconid; no wall

2=posteriorly displaced beyond protoconid, so metaconid is visible in lateral view, and share a well-defined wall

In state 0, the metaconid and protoconid share an erect cliff-like wall overlooking the trigonid that is nearly perpendicular to the long axis of the tooth. In state 1, the metaconid has been posteriorly displaced compared to the protoconid, so that they do not appear to share a well-defined wall. This migration may or may not be caused by a reduction of the metaconid, which can be observed convergently in several hypercarnivorous taxa (*Enhydrocyon*, *Megalictis*, *Simocyon*) and in pinnipeds.

123. M₁, hypoconid (Berta, 1991: character 21)

0=large or unreduced

1=vestigial or absent

124. M₁, talonid (Wolsan, character 22)

0=trigonid 1.5-2.5x longer than talonid

1=trigonid >2.5x longer than talonid

2=trigonid <1.5x longer than talonid

This character was quantified as the maximum length of the trigonid compared to the maximum length of the talonid. Trigonid length was measured from the anterior (mesial) most tip of the trigonid to the posterior most tip of the metaconid-protoconid wall. Talonid length was measured from the anterior-most tip of the metaconid-protoconid wall to the posterior (distal)-most tip of the talonid. Thus, in taxa with an open trigonid, there will be some overlap between the measured areas.

125. M₁, Entoconid (Wang et al, 2005: character 18)

0=poorly developed or absent

1= presence of a lingual notch

2=cuspidate

Ancestrally within caniformes, the entoconid of M₁ is reduced or absent. mustelids are derived in possession of a conspicuous lingual notch anterior to the entoconid, and some arctoids are derived in possessing a cuspidate entoconid.

126. M₂, size (Wang et al, 2005: character 19)

- 0= similar in size to M_1 (>0.5 length of M_1 and similar width)
- 1= significantly smaller than M_1 (<0.5 length of M_1)
- 2 = absent
- 3= larger than M_1

127. M_2 , hypoconulid (Flynn et al., 1988: characters 31, 32)

- 0=small
- 1=absent
- 2=elongated

128. M_2 , metaconid

- 0=aligned with protoconid
- 1=posteriorly

129. M_2 , metaconid

- 0=higher than protoconid
- 1=lower than protoconid
- 2=subequal

130. M_2 , entoconid (Valenciano 2016: character 72)

- 0=present
- 1=absent

131. M_2 , talonid size (Wolsan, 1993: character 27)

- 0=talonid basin distinctly longer than trigonid basin
- 1=talonid/trigonid basins subequal in length
- 2=trigonid larger
- 3=No distinction between basins

132. M_3 (Wang et al, 2005: character 22).

- 0=similar in size to M_2
- 1=smaller than M_2
- 2= absent

The M_3 is lost in musteloids and pinnipeds (Berta and Wyss, 1994).

Postcranial

133. Atlas, cervicospinal branch

- 0=present and large; well ventrally- and anteriorly-placed
- 1=absent or reduced

The foramina of the cervicospinal branch, visible within the posterior transverse foramina and travelling through the vertebral body to open medially on the vertebral canal, are distinctively large in pinnipedimorphs and some early arctoids, but are reduced in many musteloids, or even absent altogether.

134. Atlas, posterior transverse foramina (Spaulding and Flynn, 2012: character 206)

0=dorsal to transverse processes

1=In-line with or ventral to transverse processes

In state 0 the posterior transverse foramina (or vertebrae foramina) do not pass through a significant portion of the transverse processes, but rather are anteroposteriorly reduced and run through a flange dorsal to the transverse processes, as observed in canids and pinnipedimorphs. In state 1, the canal for the posterior transverse foramina is anteroposteriorly elongated and runs through the transverse process itself.

135. Axis, Cranial Articular Processes

0=confluent with dens

1=well-separated from dens by a ridge

136. Cervical vertebrae, size (modified from Berta and Wyss, 1994: character 77)

0=centrum of cervical roughly same size as lumbar

1=centrum of cervical <1.0 size of lumbar

2=centrum of cervical half the volume of that of lumbar

3=centrum of cervical larger than that of lumbar with reduced spinal canal half the size diameter of centrum

Size corresponds to breadth of centrum, anteroposteriorly and mediolaterally

137. Vertebrae, Neural Foramen

0=unexpanded

1=expanded

138. 71. Lumbar vertebrae, number (e.g., Howell, 1929)

0=7 or 6

1=5

139. Lumbar vertebrae, transverse processes (Berta and Wyss, 1994: character 80)

0=short; about as long as wide

1=long; 2-3times longer than wide

In coding this character, we selected the more posterior lumbar vertebrae with longest transverse processes.

140. Sacrum, number of fused vertebrae

0=three

1=four

2=five

3=two

141. Tail (Wozencraft, 1988: character 86)

0=long

1=vestigial

pinnipeds and some of their ancestors (*Enaliarctos*), and derived ursids display a very short tail composed of only a few caudal vertebrae (typically under 10. Other arctoids usually have many more caudal vertebrae and a longer tail.

142. Scapula, teres major process (e.g., Tedford, 1976)

0=small or absent

1=large

A scapula with an expanded posterodorsal region for teres musculature is found in many swimming and digging specialized mammals. Notably, because the scapula is a fragile element, and often not preserved in the fossil record, this character is unknown for most taxa in this analysis. An expanded scapula is seen in *Puijila* + *Enaliarctos* + *Potamotherium*, but whether this character is an autapomorphy of the pinniped clade is uncertain.

143. Scapula, post-scapular fossa (Tedford, 1976; Wozencraft, 1988, Wyss and Flynn, 1993)

0=absent

1=present, prominent

2=present, modified

The postscapular fossa is located on the axillary border of the scapula, caudad of the infraspinous fossa, and is associated with the origin of the sub-scapula muscle. The post-scapular fossa is extremely excavated in derived ursids, and present, but to a lesser extent, in many procyonids and ailurids. All other arctoids lack this fossa.

144. Scapula, metacromion process (e.g., Tedford, 1976; modified from Spaulding and Flynn, 2012: character 105)

0=small

1=large, flange-like

The metacromion process diverges from the acromion and extends posteriorly. The metacromion is very small or absent in arctoids, except for early pinnipedimorphs and mustelids.

145. Scapula, Supraspinous Fossa

0=similar size to or smaller than infraspinous fossa

1=significantly larger than infraspinous fossa

146. Scapula, spine (Berta and Wyss, 1994: modified from character 84)

0=unreduced

1=knob-like, travelling only a short distance along the scapula

147. Scapula, secondary spine (=anterior scapular ridge) of supraspinous fossa (Berta and Wyss, 1994, character 86; Furbish, 2015, character 54)

0=Absent

1=present as a spine or ridge

2=present as a scapular undulation

A well-developed secondary spine arises on the supraspinous fossa in otariids, running a

similar orientation as the scapular spine, dividing the supraspinous fossa into two nearly equally-sized halves (English, 1977). This is not to be confused with the secondary spine of the infraspinous fossa of Riggs (1945) or Tedford (1976), which appears more variably in phocids, early-diverging pinnipedimorphs, and many other arctoids groups.

148. Humerus, shaft (Berta et al., 1990) (Berta & Wyss, 1994: characters 88, 90)
0=long slender, with deltopectoral ridge not strongly developed
1=short and robust with deltopectoral ridge elevated and not significantly overhanging both sides of ridge
2=short and robust with deltopectoral ridge elevated and hanging over both sides of ridge

The development of the deltopectoral ridge is best-viewed in lateral or medial aspect. In state 0, the shaft may be somewhat flattened, but lacks the strong anterior bow (the v-shape).

149. Humerus, entepicondylar foramen (Wyss, 1988)
0=present
1=absent

150. Humerus, supinator ridge (Wyss, 1988)
0=present
1=absent or poorly developed

The supinator ridge is a plate-like extension of the lateral portion of the distal end of the humerus that serves as an attachment for forearm supinator muscles. When present, this ridge may either be sharp and crest-like (state 1) or may be little more than a rounded eminence (state 1).

151. Humerus, greater tubercle
0=rises above head
1=ventral to or in line with head

To code this character, the humerus should be held in an upright position.

152. Humerus, lesser tuberosity (Spaulding and Flynn, 2012; character 115)
0=no crest/ridge down shaft
1=with a crest/ridge leading down shaft

In state 1, the shaftward portion of the lesser tuberosity is cylindrical and projects considerably from the shaft. In state 0, this portion of the lesser tuberosity does not project significantly from the shaft, and may be represented by a thin, but sharp crest.

153. Humerus, Olecranon Fossa (Spaulding and Flynn 2012; character 107)
0=unperforated and deep
1=perforated
2=unperforated and shallow

154. Humerus, medial flexor muscle attachment

0=hangs lower than distal-most portion of trochlea
1=in line with or dorsal to distal-most portion of trochlea

155. Humerus, Diameter of distal trochlea (Kohno, 2006: character54)

0=medial lip same diameter as distal capitulum
1=medial lip diameter greater than distal distal capitulum

156. Radius, distal end (Wyss, 1988)

0=not expanded anteroposteriorly
1=anteroposteriorly flattened and expanded strongly anteroposteriorly with a small radial process
2=anteroposteriorly flattened and expanded strongly anteroposteriorly with a large radial process

157. Radius, Pronator teres process (Berta and Wyss, 1994: character 96; Boessenecker and Churchill, 2013)

0=absent
1=present, on proximal 40% of radius
2=present, distal 60% of radius

158. Ulna, Mediolateral diameter of coronoid process + lesser sigmoid notch

0=>2x smallest GSM width
1=<2x smallest GSM width
2=<1x smallest GSM width

159. Ulna, olecranon process

0=not posteriorly expanded
1=posteriorly expanded

A posteriorly expanded olecranon is observed in crown pinnipeds.

160. Digits, length (e.g., Wyss, 1988)

0=digit III manus and pes elongated
1=digit I manus and V manus and pes elongated

161. Metapodials/phalanx (e.g., Wyss, 1988)

0=keeled heads
1=flattened heads

162. Metacarpals/Phalanges (Spaulding and Flynn, 2012: character 152)

0=much longer than sum of phalangeal lengths
1=phalanges are longer than metacarpals

163. Metacarpal I, insertion of pollicle extensor

0=smooth
1=pit
2=round

164. Manus, fifth intermediate phalanx (e.g., Wyss, 1988)
 0=not reduced
 1=strongly reduced
165. Manus/pes, cartilaginous extension (e.g., Wyss, 1987)
 0=absent
 1=present
166. Pes, digit length
 0=central digits elongated
 1=digits I and v emphasized
167. Innominate, ilium (e.g., Howell, 1929)
 0=long, (ilium>obturator foramen)
 1=intermediately short (ilium roughly equal in length to or slightly longer than obturator foramen)
 2=short (length of obturator foramen significantly greater than length of ilium)
168. Ilium, separate foramen for obturator nerve (Berta and Wyss, 1994: character 113)
 0=absent
 1=present
169. Ilium, Ischiatic Spine
 0=not prominent
 1=dorsally and/or medially expanded
170. Pubic symphysis (Berta and Wyss, 1994: character 109)
 0=unfused
 1=fused
171. Insertion for Iliopsoas muscle (Berta and Wyss, 1994: character 112)
 0=on femur
 1=on ilium
172. Femur, shaft (e.g., Berta et al., 1989)
 0=long, round in cross section
 1=short, mediolaterally expanded
- In many arctoids the femoral shaft is roughly round in cross section along the length of the shaft, but in some taxa, such as *Ailurus*, the femoral shaft distally appears mediolaterally expanded. The appearance of a femoral shaft that is expanded mediolaterally, and appears “flattened” along its length is a pinniped characteristic.
173. Femur, second trochanter (e.g., Howell, 1929; (Berta and Wyss, 1994: character 116)
 0=present, long

- 1=(short) vestigial
- 2=absent

Ancestrally, the second trochanter is longer than wide (nearly rod-like) and strongly medially-projecting. While some taxa display a simple bony knob (state 1), other taxa, namely phocids, lose the second trochanter completely, leaving no trace of it.

174. Femur, Ligamentum Teres Femoris (Berta and Wyss, 1994: character 115)
- 0=Present
 - 1=Absent

175. Femur, greater trochanter height (Spaulding and Flynn, 2012: character 161)
- 0=greater trochanter lower than head
 - 1=greater trochanter higher or sub-equal than head when femur is held erect along its long axis (possibly off its condylar angle)
 - 2=greater trochanter higher or sub-equal than head when femur is positioned with distal condyles flat (possibly off long axis);

All pinnipedimorphs display an elongated greater trochanter that is extended upwards. However, phocids display an extreme state in which the greater trochanter is still level at or higher than the femoral head even when the femur is positioned so that the condyles are flat. The greater trochanter of the phocid femur is also flattened and obliquely-oriented. Such flattening and expansion was previously considered a pinniped synapomorphy, but we consider the otariids to display a different condition. The greater trochanter of the otariid is somewhat expanded, but does not depart significantly from the condition observed in other arctoids. It is difficult to discern the continuity of the greater trochanter with the lateral border of the femur, so we excluded that aspect from our character states.

176. Femur, trochanteric fossa (Berta and Wyss, 1994: character 119)
- 0=present and unreduced (concavity is readily visible)
 - 1=absent or very reduced (shallowly concave)

177. Femur, entepicondyloid ridge
- 0=absent,
 - 1=present

The entepicondyloid ridge, or medial epicondylar ridge, projects significantly from the medial epicondyle as a plate-like extension, similar to the supinator ridge of the humerus. De Muizon (1982a) reported of partial development of this feature in Semantorids, in the form of a convexity dorsal to the medial epicondyle. However, this minor degree of convexity is also observed in otariids and other musteloids, and does not depart significantly from the plesiomorphic condition, and was thus coded as 0.

178. Femur, fossa antero-proximal to trochlea
- 1=present
 - 0=absent

This fossa serves as the insertion for the articularis genus muscle, and is located on the anterior side of the distal portion of the shaft, just dorsal to the trochlea.

179. Femur, distal termination of trochlea

0=confluent with condyles

1=does not contact medial condyle

2=does not contact lateral condyle

3=does not contact either condyle

In most carnivorans, the trochlea is continuous with the lateral and medial femoral condyles on the distal surface of the femur, producing a smooth and continuous articular surface. However, in some pinnipeds, non-articular cortical bone interrupts this surface. This discontinuity can sever the connection between the trochlea and a single condyle, or disconnect both condyles from the trochlea. While it would stand to reason that variability may be explained ontogeny, this does not appear to be the case, as fully ossified adult specimens of *Eumetopias* variably display both conditions.

180. Femur, condylar angle (Berta and Wyss, 1994: character 118)

0=aligned with long axis

1=>10% off long axis

181. Patella (Berta and Wyss, 1994: character 120)

0=flat

1=conical

182. Tibia, grooves for attachment of tibialis posterior and flexor digitorum longus (see Savage, 1957; Repenning and Tedford, 1977)

0=confluent, single groove

1=multiple grooves, separated

In nearly all arctoids, the tibialis posterior and flexor digitorum longus share a groove on the distal portion of the tibia. Savage (1957) observed that these grooves are not confluent in *Potamotherium*, but are rather separated by a low crest. This condition is also observed in *Puijila*. In *Enaliarctos mealsi*, these two grooves are separated by a bump, rather than a distinctive keel or ridge.

183. Tibia, Fibula-Tibia Fusion (Berta and Wyss, 1994: character 122)

0=unfused

1=fused

184. Fibula, processus lateralis

0=unreduced, splitting peroneal tendons

1=reduced; peroneal tendons not well-separated

The processus lateralis is a keel or knob-like eminence projecting laterally from the lateral malleolus. This process, when developed, separates the long peroneal tendon from tendons of the brevis and tertius (Berta and Ray, 1990).

185. Astragalus, posterior process (e.g., King, 1983; Wozencraft, 1988: character 78)

0=absent,

1=intermediately developed

2=strongly developed

This process prevents the hindflipper from being brought plantigrade (polly). In state 2, the posterior process is remarkably elongated, paralleling the calcaneal tuber. In state 1, the posterior process is somewhat developed, but is not nearly as long as the calcaneal tuber.

186. Astragalus, Confluence of navicular and sustentacular facets

0=confluent

1=well-separated

In state 0, a portion of the sustentacular facet extends up the neck to connect with the navicular facet. In state 1, the sustentacular and navicular facets do not contact each other.

187. Astragalus, trochlear groove

0=deep (>10% of dv breadth)

1=shallow (<10% of dorsoventral breadth of trochlea)

2=No groove

188. Astragalus, trochlea

0=internal condyle higher than external

1=equal or external condyle somewhat higher

189. Astragalus, Sustentacular facet, proximal termination

0=confluent with proximal end of astragalus

1=distinctively separated from proximal end of astragalus by a groove

In condition 1, the sustentacular facet does not extend far proximally into the trochlea, and is separated from the proximal end of the astragalus by a prominent groove. In condition 0, the sustentacular facet, or at least the lateral portion of it, extends to contact the proximal end of the astragalus (trochlea). The separation in otariids is not as significant as that observed in phocids or odobenids, but a groove is still present. See Wyss, 1988 for discussion of pinniped condition.

190. Astragalus, length of neck

0=not short

1=short

State 0 refers to the lack of a projecting neck in *Ursus* and some other arctoids, so that the head barely rises above the trochlea.

191. Calcaneum, medial projection of tuber (Kohn 2006; character 59)

0=absent

1=present

192. Calcaneum, secondary shelf of the sustentaculum (e.g., Berta and Deméré, 1986)

0=absent

1=present

193. Calcaneum, peroneal tubercle – groove for tendon of peroneus longus

0=absent or very reduced
1=present

194. Calcaneum, groove for gastrocnemius upon volar surface of calcaneal head

0=strongly developed; head of calcaneal tuber concave

1=weakly developed; head of calcaneal tuber convex

In terrestrial arctoids, the groove for the gastrocnemius is well-excavated into the volar surface of the calcaneal head, whereas in pinnipeds, the volar surface of the calcaneal head is convex. The gastrocnemius in pinnipeds likely inserts parallel to the long-shaft of the bone (Howell, 1929; Polly, 2009)

195. Calcaneum, shape of head in proximal view

0=sub-rectangular

1=triangular

phocids lack the lateral tubercles of the calcaneal head for attachment of the superficial digital flexor (Polly), and thus, the head appears diamond- or triangle-shaped.

196. Cuboid, distal concave facet

0=surface is uniform

1=surface is divided by a prominent ridge, separating medial and lateral halves for IV and V metatarsal respectively

197. Cuboid, development of distal ectocuneiform facet

0=not well-developed or absent

1=present, small and square-like

2=present and anteroposteriorly elongated

All arctoids have a proximal ectocuneiform facet, but many lack the development of an antero-distal facet. This facet is entirely absent in most musteloids (though some musteloids display a vestigial facet – *Teruelictis*), and reduced in phocids. The position of the facet along the distal border varies across taxa.

198. Entocuneiform/Mesocuneiform articulation (Kohn, 2006: character 60)

0=abutting

1=overlapping

199. Palmar process of cuneiform (Bininda-Emonds and Russell, 2006: character 162)

0=present

1=absent

200. Scapholunar, head of sesamoid process

0=confluent with radial facet

1=on dorsal surface, head of sesamoid process separated from radial facet by a roughened/grooved area

201. Scapholunar, pit for magnum (Demere 1994: character 50)

0=absent

1=present

202. Scapholunar, sesamoid process orientation and robusticity

0=laterally directed and robust

1=anteriorly directed and robust

2=anterolaterally directed and reduced

3=laterally directed and reduced

203. Baculum, abruptly curving distal end (Barysnikov et al., 2003: character 1)

0=absent

1=present

204. Bacula, urethral groove on ventral surface (Barysnikov et al., 2003: character 4)

0= prominent

1=shallow or absent

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Appendix D: Data for biomechanical analyses

Table 16. List of specimens examined and measurements (mm) collected for the biomechanical analysis following the work of Samuels et al., (2013).

Family	Taxon	Institution	Specimen #	DPCL	HL	HMLD	HEB	RL	FUL	UMLD	ULOL	MC3L	MPh3P	MPh3T	FL	FAPD	FGT	FEB	TL	TMLD	TSL	MT3L	Pph3T
Odobenidae	<i>Odobenus rosmarus</i>	CMN	5357	248	325	46.	122	256	284	26.	52.	84.	72.	24.	233	33.	63.	119	369	37.	234.7	98.	43.
				.26	.96	44	.62	.23	.21	48	86	18	35	92	.89	78	98	.04	.13	69	3	35	38
Odobenidae	<i>Odobenus rosmarus</i>	USN M	2003 36	151	350	51.	144	279	314	28.	93.	88.	66.	25.	244	32.	71.	121	363	40.	253.2	131	27.
				.37	.64	56	.53	.81	.14	14	8	44	51	41	.85	65	08	.89	.9	09	7	.11	31
Odobenidae	<i>Odobenus rosmarus</i>	USN M	3249 83	266	382	59.	140	296	320	29.	104	76.	69.	24.	263	35.	71.	117	402	32.	279.5	143	27.
				.08	.08	82	.94	.41	.19	85	.24	4	05	09	.45	51	18	.31	.24	74	6	.94	33
Odobenidae	<i>Odobenus rosmarus</i>	USN M	7139	254	374	55.	146	301	346	29.	103	133	95.	43.	252	33.	73.	126	400	35.	262.7	130	39.
				.7	.47	69	.12	.24	.49	62	.69	.01	31	1	.57	33	4	.05	.35	2	4	.86	97
Otariidae	<i>Zalophus californicus</i>	ROM	00-6- 1-1	113	168	29.	62.	181	194	15.	48.	57.	61.	22.	101	16.	28.	45.	210	17.	135.5	64.	22.
				.06	.02	85	89	.33	.25	13	97	73	58	28	.42	69	27	47	.8	76	???	66	95
Otariidae	<i>Zalophus californicus</i>	USN M	4942 5	106	155	26.	57.	167	172	11.	40.	54.	45.	14.	92.	13.	30.	45.	198	17.	137.2	60.	23.
				.33	.75	59	19	.62	.59	78	94	4	31	99	74	79	27	25	.69	79	6	42	17
Otariidae	<i>Zalophus californicus</i>	USN M	A144 10	152	223	42.	88.	222	184	15.	60.	70.	60.	18.	136	17.	38.	59.	170	25.	187.5	77.	22.
				.48	.96	12	05	.81	.87	36	3	42	21	11	.97	12	43	44	.92	28	4	68	18

[Type here]

	<i>s</i>																						
Phocid ae	<i>Erignathus barbatus</i>	CMN	7523 7	89. 02	166 .08	22. 32	65. 17	139 .23															
Phocid ae	<i>Erignathus barbatus</i>	CMN	7530 8	85. 8	170 .29	26. 25	65. 41	160 .04	157 .88	13. 92	33. 5	52. 31	36. 94	46. 19	154 .25	21. 83	43. 64	76. 62	299 .95	28. 61	207.4 5	87. 13	44. 55
Phocid ae	<i>Halichoeru s grypus</i>	USN M	5044 81	88. 81	198 .69	29. 64	58. 98	164 .93	170 .99	16. 05	37. 71	45. 71	40. 18	39. 59	138 .91	19. 67	42. 06	71. 71	285 .97	30. 52	182.8	74. 22	36. 88
Phocid ae	<i>Halichoeru s grypus</i>	CMN	5282 9	77. 93	144 .12	23. 96	53. 78	141 .61	152 .66	13. 33	27. 18	37. 43	34. 65		128 .06	16. 04	40. 26	67. 38	255 .16	23. 52	166.3 9	72. 51	
Phocid ae	<i>Halichoeru s grypus</i>	USN M	4464 05	92. 82	166 .75	27. 67	60. 53	262 .45	168 .97	15. 54	39. 07	43. 25	39. 27	43. 36	144 .12	17. 92	43. 79	70. 7	279 .24	25. 33	187.4 4	68. 75	32. 61
Phocid ae	<i>Halichoeru s grypus</i>	CMN	5282 9	77. 36	139 .45	26. 79	50. 7	142 .04	152 .76	14. 48	24. 46	40. 06			127 .66	16. 66	39. 25	67. 4	260 .6	24. 69	170.3 3	67. 32	
Phocid ae	<i>Pusa Hispidia</i>	CMN	7509 5	63. 24	111 .06	17. 17	38. 51	105 .62	116 .06	9.2 1	20. 07	34. 78	28. 58		97. 84	11. 3	28. 15	47. 5	195 .02	15. 81	122.3 8	52. 17	
Arctoi dea	<i>xxxPotamo therium valetoni</i>	FSL	2139 02	36. 2	66. 8	8.0 2	23. 01	58	64. 9	4.1 8	17. 6	25. 4	20		64. 8	7.8	12. 7	24. 95	92	5.7	47.6	40. 5	
Otariid ae	<i>Callorhinu s ursinus</i>	CMN	???	137 .91	201 .65	29. 79	72. 11	186 .1	199 .65	22. 66	64. 94	56. 21	59. 3	19. 56	127 .35	16. 83	30. 29	55. 88	212 .82	19	131.7 2	69. 03	20. 62

[Type here]

Otariid ae	<i>Euetopias jubatus</i>	ROM	2035 6	212 .89	309 .7	56 08	97 22	288 .71	306	28 06	112 .68	104 .94	121 .28	31 41	211 .51	26 97	55 84	80 69	212 .47	46 29	216.2 4	113 .71	
Phocid ae	<i>Cystophora cristata</i>	USN M	1611 6	83 5	156 .64	24 87	65 31	198 .97	167 .96	15 44	36 99	53 56	65 41	41 34	150 .44	20 3	42 02	73 25	317 .14	26 04	208.4 1	91 1	39 1
Otariid ae	<i>Arctocephalus forsteri</i>	USN M	5504 79	119 .28	174 .55	28 26	63 64	159 .45	170 .19	12 03	50 22	52 84	56 61	16 07	100 .79	11 88	28 23	41 01	198 .66	15 31	120.6 9	60 96	26 32
Phocid ae	<i>Hydrurga leptonyx</i>	USN M	3969 31	94 55	179 .59	38 81	69 07	183 .48	190 .06	21 51	29 29	61 45	77 67	29 27	142 .5	26 18	44 09	81 09	288 .68	32 64	162.2 1	85 59	50 32
Phocid ae	<i>Leptonycho tes weddellii</i>	USN M	5501 18	89 66	150 .79	26 7	58 99	180 .31	190 .65	15 04	28 79	52 77	55 63	29 7	134 .42	20 77	37 49	71 46	292 .64	30 05	184.6 1	72 19	35 67
Phocid ae	<i>Monachus schaunslan di</i>	USN M	2752 06	66 8	130 .76	25 6	47 33	133 .67	129 .94	12 6	21 32	47 25	58 23		105 .56	19 37	37 12	63 63	255 .3	25 32	173.1 2	60 85	
Phocid ae	<i>Pagophilus groenlandi ca</i>	USN M	3517	69 81	125 .38	22 56	42 03	129 .21	138 .43	11 1	32 94	38 92	34 09	24 3	107 .04	14 21	31 77	59 34	165 .4	21 17	165.0 6	67 6	35 29
Arctoi dea	<i>xxxPuijila darwini</i>	CMN	NUF V - 405	57 13	97 96	8.5 4	29 86	74 52	77 58	4.8 9	19 74	35 65	13 9	10 6	90 15	9.4 9	25 53	25 73	110 .79	6.7 1	50.41	43 87	11 4

[Type here]

Table 17. List of scores for the functional indices used for the biomechanical analysis following Samuels et al. (2013).

Family	Taxon	Ecology	SMI	BI	HRI	HEI	URI	OLI	MANU	CLA	CI	FRI	GI	FEI	TRI	TSI	PES	IM
Phocidae	<i>Pusa Hispida</i>	Hindlimb - dominate d aquatic	0.56 94	0.951 0	0.154 6	0.346 7	0.079 4	0.172 9	0.8217		1.993 3	0.115 5	0.287 7	0.485 5	0.081 1	0.627 5	0.533 2	0.739 9
Arctoidea incertae sedis	<i>Potamotherium</i>	Unknown	0.54 19	0.868 3	0.120 1	0.344 5	0.064 4	0.271 2	0.7874		1.419 8	0.120 4	0.196 0	0.385 0	0.062 0	0.517 4	0.625 0	0.795 9
Otariidae	<i>Callorhinus ursinus</i>	Forelimb- dominate d aquatic	0.68 39	0.922 9	0.147 7	0.357 6	0.113 5	0.325 3	1.0550	2.875 8	1.671 1	0.132 2	0.237 8	0.438 8	0.089 3	0.618 9	0.542 0	1.139 9
Otariidae	<i>Eumetopias jubatus</i>	Forelimb- dominate d aquatic	0.68 74	0.932 2	0.181 1	0.313 9	0.091 7	0.368 2	1.1557		1.004 5	0.127 5	0.264 0	0.381 5	0.217 9	1.017 7	0.537 6	1.411 4
Phocidae	<i>Cystophora</i>	Hindlimb - dominate d aquatic	0.53 31	1.270 2	0.158 8	0.416 9	0.091 9	0.220 2	1.2212	1.672 9	2.108 1	0.134 9	0.279 3	0.486 9	0.082 1	0.657 2	0.605 6	0.760 5
Otariidae	<i>Arctocephalus forsteri</i>	Forelimb- dominate d aquatic	0.68 34	0.913 5	0.161 9	0.364 6	0.070 7	0.295 1	1.0713	2.150 8	1.971 0	0.117 9	0.280 1	0.406 9	0.077 1	0.607 5	0.604 8	1.115 4
Phocidae	<i>Hydrurga leptonyx</i>	Hindlimb - dominate d aquatic	0.52 65	1.021 7	0.216 1	0.384 6	0.113 2	0.154 1	1.2640	1.543 5	2.025 8	0.183 7	0.309 4	0.569 1	0.113 1	0.561 9	0.600 6	0.842 0

[Type here]

Phocidae	<i>Leptonychotes</i>	Hindlimb	0.59	1.195	0.177	0.391	0.078	0.151	1.0542	1.559	2.177	0.154	0.278	0.531	0.102	0.630	0.537	0.775
		-	46	8	1	2	9	0		6	1	5	9	6	7	8	0	3
		dominate																
		d aquatic																
Phocidae	<i>Monachus</i>	Hindlimb	0.51	1.022	0.195	0.362	0.097	0.164	1.2324		2.418	0.183	0.351	0.602	0.099	0.678	0.576	0.732
	<i>schaunslandi</i>	-	09	3	8	0	0	1			5	5	6	8	2	1	4	8
		dominate																
		d aquatic																
Phocidae	<i>Pagophilus</i>	Hindlimb	0.55	1.030	0.179	0.335	0.080	0.238	0.8759	0.966	1.545	0.132	0.296	0.554	0.128	0.997	0.631	0.934
	<i>groenlandica</i>	-	68	5	9	2	2	0		0	2	8	8	4	0	9	5	5
		dominate																
		d aquatic																
Phocidae	<i>Erignathus</i>	Hindlimb	0.51	0.889	0.144	0.388	0.088	0.212	0.7062	0.829	1.944	0.141	0.282	0.496	0.095	0.691	0.564	0.699
	<i>barbatus</i>	-	97	7	4	2	2	2		2	6	5	9	7	4	6	9	7
		dominate																
		d aquatic																
Odobeni	<i>Odobenus</i>	Hindlimb	0.64	0.791	0.149	0.386	0.090	0.280	0.7937	2.197	1.543	0.136	0.281	0.486	0.094	0.670	0.506	1.014
dae	<i>rosmarus</i>	-	22	0	0	7	2	3		4	7	0	1	8	9	9	9	4
		dominate																
		d aquatic																
Phocidae	<i>Halichoerus</i>	Hindlimb	0.51	1.095	0.166	0.345	0.092	0.199	0.9140	1.094	2.006	0.130	0.306	0.514	0.096	0.654	0.524	0.839
	<i>grypus</i>	-	91	6	5	1	0	0		6	4	5	9	5	3	0	9	7
		dominate																
		d aquatic																
Otariidae	<i>Zalophus</i>	Forelimb-	0.67	1.043	0.179	0.380	0.076	0.272	0.9154	2.446	1.752	0.143	0.292	0.453	0.104	0.839	0.612	1.228
	<i>californicus</i>	dominate	89	9	9	0	6	3		6	8	8	8	5	8	4	3	1
		d aquatic																
Arctoidea	<i>Puijila darwini</i>	Unknown	0.52	0.760	0.087	0.304	0.050	0.202	0.3590	0.933	1.229	0.105	0.283	0.285	0.060	0.455	0.486	0.858
incertae			80	7	2	8	2	8		0	0	3	2	4	6	0	2	4
sedis																		

[Type here]

Table 18. List of measurements used in the biomechanical analysis following Bebej (2009). All measurements are in mm.

Taxon	Sex	Specimen Number	Thorax	Lumbus	Scapula	Humerus	Radius	Mcarp III	Man piii1	Man piii2	Ilium	Femur	Tibia	Mtars III	Ped piii1	Ped piii2
<i>Puijila darwini</i>	M	NUFV- 405	31.25	13.90	9.25	9.80	7.45	3.57	2.71	1.79	5.63	9.02	11.08	4.39	2.69	1.87
<i>Potamotherium valetoni</i>	?	FSL- 213902	21.95	12.24	6.22	6.66	5.80	2.54	2.00	1.63	4.4	6.49	9.20	4.05	2.21	1.50

[Type here]

Appendix E: Morphological data matrix for phylogenetic analysis

Acrophoca

0021120020100320?0012?100110313?12100???4050310002012010020?21?2?210?1?1?2???110?0?10?00?0?015?2?????????12???
???0001???????2?????20001?1111100?101111121022?111101?12111112121011101002111100011101???????

Ailurus

0000110010111120000301201230200000000???00310130100010?00101100000010?0000?10020100000111111030?101110000000
01011000(0 1)04200022321100210020000011100000010010000000000?000000000000000000001011100010000000???

Allocyon

001?111010?1??2?0???0?1???00?0?000000???1010?2302?000???10110?????0?????????010?000??0??00030?01???1?2000001101
?0?00?200?????1??

Allodesmus

00011211?2100?3000210200010(01)301011100???2120?230?2101?1?110?11?0?110010?1?12?11120????0?2??11??33???????0?210
???1?01?????????????????0031110?0?0102111112102111110?1111?1011?11???11001101111001??1?1??01??

Amphicticeps

001??110?01????0001011???0000000000???2011?1301?00?????????0???000000??????0?????00000?0000000(0
2)00101000111101?000002000001??0?3(1 2)??

Amphictis

0000?100?0?1????0?0?0?1???00?0?00000????031?1?0?0001???010??0???0000??????0101000?010?0000000000??00200000???1
???002000203?11102??

Arctocephalus

0111100000100230320122100021300010100????2110?130?3001??120111010?0?0?????1???01130001100000115033120?212011002
1011010111010102?????2100311011000101211012102111???????11010111?101011101011010011100000?????

Arctodus

000011000100110?00?33010123020?00?000???2000?120200020??100110???000000?0???000?0??100?0???03200?????????0?????
??0?????????2?????????????0??

Brachypsalis

0000100?00000?0?00000?001200?1?01000?????00(01)?1???0?02?0?010?00?0??0?0?00?????011?01000000001000?00200200120(0
1)1211110?00312010111??1?2?????????????????0001010?0?????0?????????0100?01?0?????01011000????????????

[Type here]

E. mitchelli

00211?0000011?31030?03???0?300?1011?????0?23011002??0010?11?0?1??????1??????????0000002101120121000111???1
??

E. tedfordi

002?1?00?0111?300?0?3?10?00?300?1111????2010?230?1002???1?0?0????0001???021??????????000002101?????????111???1?
???

Enhydra

000?1000?0110?31000?(03)?10?230210010001000?00?01000110201?00001100000000000?0001010000001000013202211121102
02?????11?010020002?11??132011200000?011000011100?200?00?0?00000000?0?00??1?000?1100000100?00100200

Erignathus

1020120021100331100(01)22101110?13112100?0?4000?2010301201002002112221011111222111120000100000015022120?21201
12?????11?000002?0102?????20002111111000001001121022111010001201111212?1031010020111000111010110301

Eumetopias

0121100000100230320022100021300010000?012110013001002001201?1010101001001102101121001100000015033120?2120122
????110101032?1102?????20003110?10001012110121021111110111100101011101(2 3)111010010100111010001?001

Gulo

000011100001011000000?101030210000001?0?30030130101021000100?0000000000000000010000000000001010002002001202
????100000001001?11?1?32110100100001???00010?1000000000000000000010000000000110000000000100110

Halichoerus

0020120020100331100102101110313112100?0?400032010311201?020021?2121011111222111020000100000015032120?2120122
????11?001002?0102?????2000111111100000100112002211101000120111121201111010020111000111010110301

Hemicyon

?????????0??
?01110(0 2)0101100??

Hesperocyon

00000200?000000?000101????00?000000001000001?010?00001?010000?????????????????01000?0?00000000000000000000010
110000011000001102101010?????????????010100?0????????????????????????????000?0000?0???0000?????????0

[Type here]

Imagotaria

0?21101102110?3?131112000310302011000???21103230?1000?00110?11?1?110010?11?2101130?011001????2033????????110??
?110(0 1)0?511?1102?????00??0??1???1001110121132111111???1????????1????0???101010101101?1??10??

Kolponomos

000001(01)(01)2011023001100?100000302010100???1010?230?1100??000?10??????????????0112110?00111013201111121200
0011101100002001022011?132??0?0??

Lontra

00011100?00??1300?0?0?10?230210010001001?0030100011021?1000011002000000000000010?0000001?00013?0022012?01202?
???100010000002211????2111100000101100000100000?0000?0000000000001000000000?1010000?0000100210

Megalictis

000011000001??2?0?0?0?10?200?10000000????020?100?0102???010??0???00000?????010?000000100010010002002011001121
0100000322?0111?0?0?20?????????1????00100000000?0?0???0???0001000?0?0000?1???000?0?????????

Mephitis

0001020010001?20000?0?10?001310010000010002021100010201100000000000000000001?0101010000100001720002010000002
????100010000102211?01321?0000030001?00010100?0000000000000000000?0000?00000000111000010000?00201

Mirounga

000112003011023130112210111?313111100????000?10102112??002002010121011????????01100010100000015033120?212?122??
??110101002?1?02?????2?01?????000110111112102201????????2011112101013101012011100011100???????

Monachus

0021120030100230300102(01)01110313112100?0?40003200?20120101201211012101111?122101000010000000115123120?212?1
12????110001411?1102?????2101?111010001101111121022?1111?101211111211101310(0 1)01211110001110000?0000

Mustelavus

000?11?0?00????0?0?????????0?000?000?????000?1?0??000?????????0?????000?????01000????000?010000000000100010????1?
0?005100?00101?22??

Neotherium

00211??002110?3?13111??0310?02?10?10????11031?0?1000?????????1?1?1????????????01120?0?1001????2012????????????1????11
000????1??1????????2????????????????????????????13????????????????????????????????????10101010?0011??10??

[Type here]

Neovison

00111?000001?12?000?0?1?1?31310010001?0000030100001011??010?0?00?0000000000?0010000?0001?0001000002002?01202??
??100?10000000?11??1?21?010?0000011000001001000000?00?0000000010100000000000011000000000100210

Odobenus

0001110132?00230231112000310302111000?0?21103230010000?111011111211001011112111131?11?00100015033????????32?
???11110?01????2?????00?1101?10001001110121132111111111(0 1)010111110021100110101010110111011001

Oligobunis

0?0???0010?00?0?000?0?101?00?000000????000?100?0?00?0?0100?0?????????????????0?0?00000000?100000020020100011210
1?00000?10?111?0?22??

Otaria

01211001001(01)0230320222100021300010100???2110?130010020?1201?10?01010010??1???0113000?10000001??3??????????22
????110101??????2??11111012????????????????????????

Paragale

0010110?00010?2?00010?1??230?10000001000?003?110?1102??010?00?0?00000????????????00?00000011000012002001102???
?1?0????????12????2??

Phoberogale

001011?0?00111000?0????0?00?0?0000000102011?10020002???010100?0??00000?0?0?010?0?0100?000?0700000001020000010
?10000002120(0 2)00100(0 1)01?????0?0?12????00?1000000000000??0?0??00000?0?0?00?0?01?000000????????

Phoca

10111200201003311001021011103131121000014000320103112010020021?222101111?222111020000100000015022120?21201?2
????11000111110?02????20001?11111000001001120?221110100012011112120111101?020111000111?101?????

Pinnarctidion

001112000(12)111?31030002100100(23)01?1?1100012010323012002110100?11?01110010?????0???0?01?00001012111(0
1)201212001102101????????????????????????????????000?001101121????????????????100?0?111????????????????????

Piscophoca

0?2012002?100331?0012?10111?31311??0????4050320??2112010020?21?2??10?1????????0100?010?000?????12?120?2120122????
1???0????????2????2100?????10?110111112102211??????201?1?????????101????????????????????

[Type here]

Plesiogale

0000110000?10?2?00?10?1??200?10000001?????3?1?0??01??010?00?0?00?000?????0??0?0?001000110000120020011020???
1?0?????????12????22?????????????0??

Pontolis

002?1??1??10?3??111?10?310?02?1000????2110?1?0?1?0?????????????1?1?????????????0?131?????010?????32??????????11????1?1
?????????1?????????????????0?????????????????1?????1?????1?????1?????????????1?????????????

Potamotherium

(01)02111(01)00(01)0112300001(03)(03)10000031001001010120003100?1002010100100?0?(01)00010000011010000000000000007
00012002010(01)011210100000110200011?1132000100000101000100002100210001000010?00100100101001000?1100011001??1
0101

Procyon

(01)00?10001000102000000120000021000000000020021110001020010100000000000000001001000100000001130000010020
00000001000000101122020000211010(0 1)10011?00000?1000000?00000?00?000000100?00000000011?0000?00?100211

Promartes

000?000000010?200?0?0010?000?10000000000?000?100?01000?0?10000?0?0000000?0??010?000000000100000120020110010?
??1?00000210101111?1?2??0??0?010????000?01?0?00?0?00?0?0??010100000?00?0?1?????00??????????

Promephitis

0001010010?0??2?000?0?????00?1000?0001100020?100001021?0000??????000??0??0100?100?01000017200020100(0
1)0202??10??1000?102(0 2)11?1132??

Proneotherium

002112000211023?13101?000000302010110????2110?130?1000??110?1?????00010?????011201011001010120(0
1)1?????????010??1100011111101?????200?0?11?????????????????2??0?????10??1?0??0?1?00?10100010110111?????

Prototaria

002112?002111?3?1210(12)21?0000302?1??10????211031?021000?00?0??1??1?1?0??????????????1??000??????01?????????010??
?1?0??

Pteronarctos

012112100211123(01)1(23)00(03)0100000300010110??21103130?1002??010?10??12?010??02101020101000001002111?????
??111??1?000????11101?????2000?0?0??100?02??11??

[Type here]

Appendix F: Molecular sequence data for phylogenetic analysis

Ailurus

TGATGCCCCCACGGAAGGCCCGTCAGCTCCACCACCCCGTATGTGGAGGACACCCCGAGCCGCCCTCCAT
GACTTCTACTGCAGCAGGCTTCTAGACCTGGTTTTCTGCTAGATGGCTCTTCCAAGCTGTCTGAGGATGAGTTTGGAGT
GCTGAAGGCCTTCGTGGTGGGCATGATGGAGCATCTGCACATCTCCAGAAGCGGATCCGCGTGGCGGTGGTGGAGTA
CCACGACGGATCCCACGCCTACATTGAGCTCCAGGACCGGAAGCGACCCTCGGAGTTGCGGCGCATTGCCAGCCAAGT
GAAGTACGTGGGCAGCGAGGTGGCTTCCACCAGCGAGGTCCTGAAGTACACACTGTTCCAGATCTTCAGCAGGATCGA
CCGCCCCGAAGCGTCCCGCGTTGCCCTGCTCCTCATGGCCAGMCAGGAGACCCCGAGGCTGGCCCCGCAATTTGATCCG
CTATGTGCAGGGCCTGAAGAACAAGAAGGTCACCGTGATCCCCGTGGGCATCGGGCCCCATGCCAACCTCAGGCAGAT
CCGCAACATTGAGAAGCAGGCCCCCGAGAACAAGGCCTTCGTGCTCAGCGGTGTGGACGAGCTGGAGCAGCGAAGGG
ACGAGATTATCAACTACCTGTGTGACCTTGCTCCCGAAGCACCTGGCCCTACTCGGCAGCCCCCTGTGCTGGCGGTAC
CGTGGGTCCAGAGCTCTCAGGGGTCCCGTCATCGGGACCCAAAAGGAACTCCATGGTTCTCGATGTGGTGTTCGTCCTG
GAAGGCTCGGACAAAATTGGCGAGGCCAACTTTAACAAGAGCAAGGAGTTCATGGAGGAGGTGATTCAGCGGATGGA
CGTGGGCCAGGACGGCATCCACGTACAGTGCTGCAGTACTCCTACGCCGTGACTGTGGAGTACACCTTCAGCGAGGC
CCAGTCCAAGGGGGAGGTCTGCAGCACGTGCGGGAGATCCGATTCCGGGGCGGCAACAGGACCAACACCGGGCTGG
CCCTGCAGTACCTGTCTGAGCACAGCTTCTCTGTCAGCCAGGGGGACCGGGAGCAGGTCCCTAACCTGGTCTACATGGT
CACAGGAAACCCCGCCTCTGATGAGATCAAGCGGATGCCTGGCGACATCCAGGTGGTGCCATCGGAGTGGGCCCTCA
CGCCGATGTGCAGGAGCTGGAGATAAAGACAGAATGAATGTAGAAAAGGCTGAATTCTGTAATAAAAGCAAACAGCC
TGGCTTAGCAAGGAGCCAACAGAACAGATGGGCTGAAAGTAAGGAAACATGTAATGATAGGCAGACTCCCAGCAGAG
AGAGAAAGGTACTTCTGACTGCCGATCCCCTGTGTGGGAAAAAAGAACTGAAGACGCAGAAACCTCCATGCTCTGACA
GTCCTAGAGATTCCCAAGATGTTCCCTTGATAAACTGAATAGTAGCATAACAGAAAGTTAATGAGTGGTTTTCCAGAAG
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Canis

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Enhydra

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Lontra

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Mephitis

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Neovison

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Odobenus

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Phoca

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Procyon

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Taxidea

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Ursus

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