

A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia

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Modern pinnipeds (seals, sea lions and the walrus) are semi-aquatic, generally marine carnivores the limbs of which have been modified into flippers. Recent phylogenetic studies using morphological and molecular evidence support pinniped monophyly, and suggest a sister relationship with ursoids^{1,2} (for example bears) or musteloids^{3–7} (the clade that includes skunks, badgers, weasels and otters). Although the position of pinnipeds within modern carnivores appears moderately well resolved, fossil evidence of the morphological steps leading from a terrestrial ancestor to the modern marine forms has been weak or contentious. The earliest well-represented fossil pinniped is *Enaliarctos*, a marine form with flippers, which had appeared on the northwestern shores of North America by the early Miocene epoch^{8,9}. Here we report the discovery of a nearly complete skeleton of a new semi-aquatic carnivore from an early Miocene lake deposit in Nunavut, Canada, that represents a morphological link in early pinniped evolution. The new taxon retains a long tail and the proportions of its fore- and hindlimbs are more similar to those of modern terrestrial carnivores than to modern pinnipeds. Morphological traits indicative of semi-aquatic adaptation include a forelimb with a prominent deltopectoral ridge on the humerus, a posterodorsally expanded scapula, a pelvis with relatively short ilium, a shortened femur and flattened phalanges, suggestive of webbing. The new fossil shows evidence of pinniped affinities and similarities to the early Oligocene *Amphicticeps* from Asia and the late Oligocene and Miocene *Potamotherium* from Europe. The discovery suggests that the evolution of pinnipeds included a freshwater transitional phase, and may support the hypothesis that the Arctic was an early centre of pinniped evolution.

Among mammals, the land-to-sea transition has occurred several times with varying completeness, as shown by cetaceans, sirenians, desmostylians, pinnipeds and sea otters. This transition is characterized by innovations associated with most aspects of life, including locomotion, feeding and reproduction. The fossil record has documented early stages in some of these transformations, most successfully in that of whales from terrestrial artiodactyls¹⁰. The early evolution of pinnipeds has been more difficult to resolve. The earliest widely accepted fossil pinniped, *Enaliarctos*, of the early Miocene of western North America, is similar to modern pinnipeds in that it is a short-tailed marine specialist with well-developed flippers⁹. With *Enaliarctos* considered the earliest pinniped, there exists a major transformational gap between a terrestrial ancestor and the appearance of flippered pinnipeds. Indeed, most studies of pinniped relationships and evolution do not consider the critical first evolutionary stages that ultimately gave rise to this successful group of marine carnivores.

New evidence on pinniped origins is provided by the discovery of a small mammalian carnivore, *Puijila darwini* gen. et sp. nov., in Miocene deposits of the Haughton Formation of Devon Island,

Nunavut, Canada (Fig. 1). *Puijila* is a morphological intermediate in the land-to-sea transition of pinnipeds and provides new evidence concerning the evolution and biogeography of the earliest pinnipeds.

The Haughton Formation, located within the Haughton impact structure at 75° 22' N, 89° 40' W, consists of post-impact lake deposits that accumulated in the crater. The formation is up to 48 m thick, and is mainly within the western half of the impact crater. Fission-track and ⁴⁰Ar–³⁹Ar furnace step-heating dating of the structure yielded an impact age between 24 and 21 Myr, that is, late Oligocene epoch to early Miocene epoch¹¹, although another ⁴⁰Ar–³⁹Ar analysis of the structure favoured a late Eocene age of 39 Myr (ref. 12). The previously reported vertebrate fauna from the lake deposits includes at least two taxa of freshwater teleost fishes, one bird and four mammalian taxa (shrew, rabbit, rhinoceros and small artiodactyl). An early Miocene (Aquitanian/late Arikarean) age for this fauna is

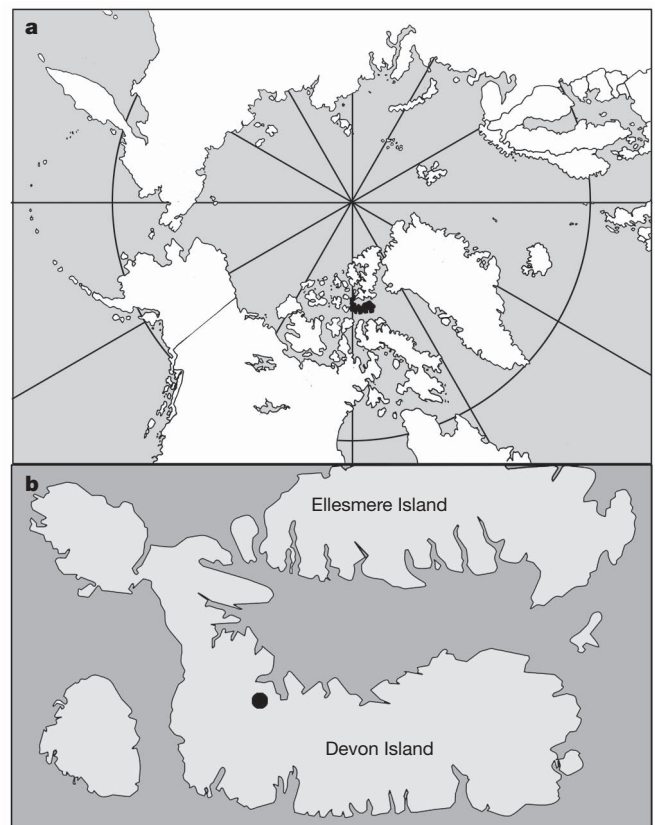


Figure 1 | Geographic location of fossil site. a, Devon Island in a polar projection. **b**, Haughton impact structure on Devon Island.

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supported particularly strongly by the rabbit (family Leporidae) and shrew (family Heterosoricidae)¹³. The palaeobotanical record suggests that the palaeoenvironment around the lake comprised a forest community transitional between a boreal and a conifer–hardwood forest, in a cool temperate, coastal climate with moderate winters¹³. *Puijila darwini* is the first mammalian carnivore found in the Houghton lake deposits.

Puijila darwini gen. et sp. nov.

Etymology. *Puijila* (Inuktitut): young sea mammal, often referring to a seal; *darwini*: for Charles Darwin, who wrote with his usual prescience, “A strictly terrestrial animal, by occasionally hunting for food in shallow water, then in streams or lakes, might at last be converted into an animal so thoroughly aquatic as to brave the open ocean”¹⁴.

Holotype. NUFV 405 (Nunavut Fossil Vertebrate Collection, housed at the Canadian Museum of Nature, Ottawa, Ontario, until facilities are available in Nunavut), partial skull and postcranial skeleton (about 65% complete) of a single male individual (Figs 2 and 3).

Locality and horizon. Canada, Nunavut, Devon Island, Houghton Formation. Field number Dev-07-07-20B. Early Miocene (Aquitanian, European mammal zones MN1-3; Arikarean NALMA).

Diagnosis. Arctoid mammal. Skull having short, high rostrum; large infraorbital foramen; large orbit; zygomatic bone strongly arched dorsally; broad palate with elevated median ridge; alisphenoid canal and small postglenoid foramen present; prominent mastoid processes. Mandible having deep masseteric fossa and coronoid process wide anteroposteriorly. Dentition: 2?/2, 1/1, 4/4, 2/2; I³/I₃ much larger than I²/I₂; M¹ with strong parastyle; small, single-rooted M² in line with lingual side of M¹; M₁ paraconid larger than metaconid, talonid has lingual ridge in place of entoconid; M₂ small, single rooted. Scapula expanded posterodorsally; humerus with prominent deltopectoral ridge; manus and pes with long metapodial I, flattened phalanges; relatively short ilium and femur. Combined head and body length estimated to be about 110 cm. For differential diagnoses see Supplementary Information.

Taken together, the dental, cranial and postcranial characters of *Puijila* suggest that a phylogenetic analysis including *Amphicticeps shackelfordi*, *Potamotherium valletoni* and *Enaliarctos* would be appropriate. This analysis of *Puijila* and early arctoids (including pinnipeds, musteloids, ursoids and their fossil near-relatives) recovered a clade uniting *Amphicticeps*, *Potamotherium* and *Puijila* with *Enaliarctos* (Fig. 4).

Within the group, *Amphicticeps* is most basal. *Amphicticeps* is represented by cranial and mandibular remains, but no postcranial elements, from Oligocene Hsanda Gol deposits from Mongolia². Previous phylogenetic assessments had aligned this taxon tentatively with ursoids², and most recently as the sister taxon to a clade of pinnipeds plus all other musteloids⁷. *Amphicticeps* resembles *Puijila* in a range of characters, including having a skull with short, broad rostrum; a short infraorbital canal; an anteroposterior median ridge on an elongate palate; a small M², aligned with the lingual side of M¹; M³ absent; and M₃ absent (in some *Amphicticeps* specimens). If *Amphicticeps* is a basal pinniped, then the clade originated by the

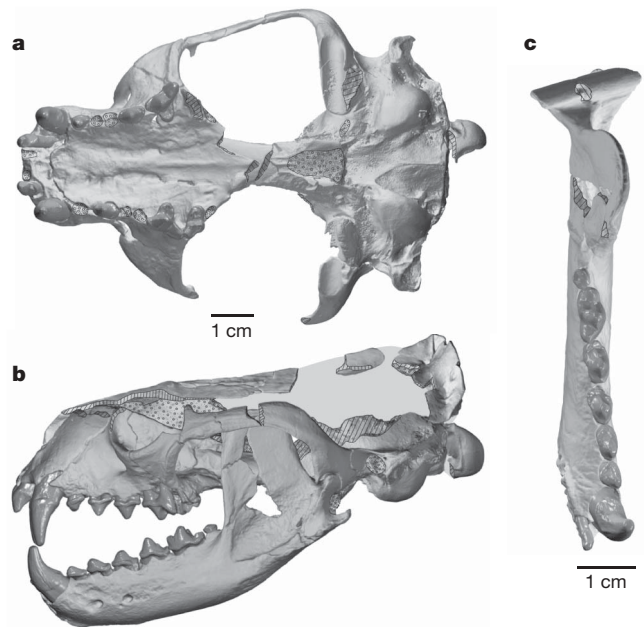


Figure 3 | *Puijila darwini* skull (NUFV 405, holotype). **a**, Palatal view of skull; **b**, lateral view of skull and mandible, left side; **c**, occlusal view of left mandible. Stippling represents matrix, hatching represents broken bone surface. The images are of three-dimensional scans. The brain case was scanned using computed tomography, whereas all other elements were surface scanned.

Oligocene in Eurasia. Previously, estimates on the origin of pinnipeds based on the fossil record had suggested a late Oligocene origin¹⁵, but a recent molecular-clock estimate is consistent with an early Oligocene origin³.

The clade of *Puijila*, *Potamotherium* and *Enaliarctos* shares a number of characters including a posteriorly expanded hard palate, an enlarged infraorbital foramen, a shelf-like protocone on P⁴, a reduced and lingually situated M², a robust deltopectoral ridge on the humerus and a posterodorsally expanded scapula. The lack of postcranial evidence for most basal arctoids restricts comparisons of most other skeletal regions.

Potamotherium valletoni is relatively well known from thousands of isolated bones, but no complete associated skeleton, from early Miocene (MN1-2) freshwater lakes in central France¹⁶. Early descriptions cast *Potamotherium* as a lutrine mustelid, an assignment contradicted by its lack of derived lutrine dental features¹⁷, a postcranial skeleton more specialized for aquatic life than that of modern otters^{8,16} and an ear region of primitive arctoid–amphictoid type¹⁸. *Potamotherium* has also been considered, among other assignments, a member of a musteloid stem group¹⁸, an arctoid incertae sedis¹⁹, an oligobunine^{2,17} and a pinniped in the family Semantoridae^{4,20,21}.

Among fossil pinnipeds for which postcrania are known, *Puijila* is the least specialized for swimming. The well-known *Enaliarctos* is

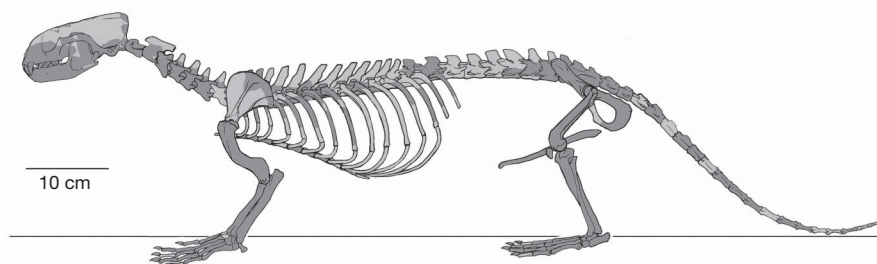


Figure 2 | *Puijila darwini* skeleton (NUFV 405, holotype). Reconstruction of skeleton showing preserved bones in dark grey.

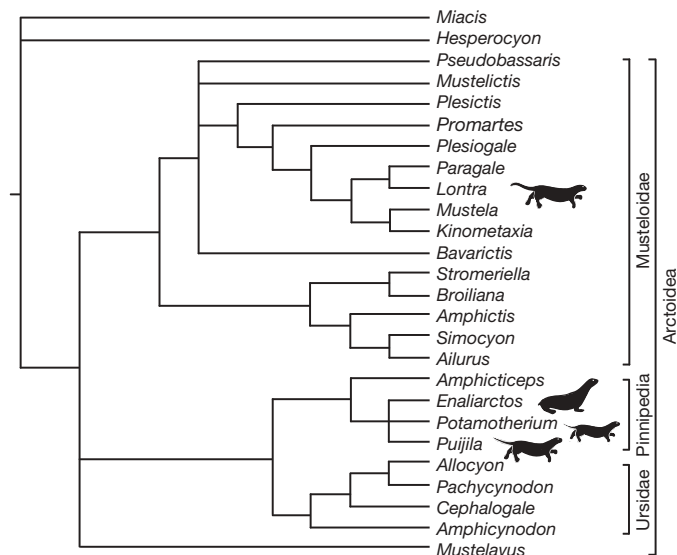


Figure 4 | Phylogenetic position of *Puijila* within Arctoidea. Strict consensus cladogram of the eight most parsimonious trees. See Methods and Supplementary Information for additional details.

most similar to modern pinnipeds, having a streamlined body, a reduced tail and limbs that were highly modified to form flippers. In contrast, *Puijila* did not possess flippers, its feet were probably webbed, it had a long tail and its limb proportions were generally similar to modern otters. A comparison of limb proportions of *Potamotherium*, *Enaliarctos* and *Puijila* with those of living arctoids finds that the limb proportions of *Puijila* are much more similar to those of land-dwelling arctoids, such as *Martes* (fisher) and *Mephitis* (skunk), than to either *Potamotherium* or *Enaliarctos* (see Supplementary Information for comparison of limb proportions). *Potamotherium* is similar to *Puijila* in that its overall form was otter-like, but its musculoskeletal system appears to be more specialized for swimming¹⁶.

Of the living arctoids, the postcranial skeleton of *Puijila* appears most similar to that of the extant river otter *Lontra canadensis*. In *Lontra* and *Puijila*, the femur is slightly shortened and the humeral shaft is strongly curved and bears a robust deltopectoral ridge. *Puijila* exceeds *Lontra* in the degree of specialization of the shoulder region, having a humerus with a slightly better-developed deltopectoral ridge and a more derived scapula, which is expanded dorsoposteriorly. A low ridge within the infraspinous fossa indicates the presence of an expanded teres musculature, a condition also seen in *Potamotherium*¹⁶, *Enaliarctos*⁸ and other pinnipeds²⁰.

The proportions of the manus and pes elements differ in *Puijila* in comparison with *Lontra*. In *Puijila*, the manus is longer. Also, for both the manus and pes, the first digit in *Puijila* is elongate relative to the other digits (although shorter than the second digit). The pedal phalanges are much longer in *Puijila* than in *Lontra*, and are dorsoventrally flattened near their distal ends. Phalangeal flattening may be associated with the presence of webbing between the digits. In the sea otter *Enhydra*, the almost flipper-like hind foot has flattened phalanges. Flattened digits are also present in the manus and pes of other pinnipeds, including *Potamotherium* and *Enaliarctos*. The tail of *Puijila* appears to have been shorter and more gracile than that of *Lontra*; in this regard, *Puijila* is also similar to *Potamotherium*.

The presence of enlarged, probably webbed feet, robust forelimbs and an unspecialized tail suggests that *Puijila* swam quadrupedally using its webbed fore and hind feet for propulsion. It was almost certainly not specialized for swimming under water using simultaneous pelvic paddling, as seen in *Lontra*. Mammals that swim using simultaneous pelvic paddling do so without the aid of their front legs,

relying instead on simultaneous propulsive thrusts of the hindlimbs in combination with dorsoventral tail (and sometimes body) undulations²². In contrast, most living pinnipeds swim using one of two disparate modes: true seals (Phocidae) use their hind feet in a side-to-side pelvic oscillation, whereas fur seals (Otariidae) oscillate their fore flippers, in a movement akin to flying²³. As a possible quadrupedal swimmer, *Puijila* represents a form that could have given rise to both of the major swimming modes observed in pinnipeds today. *Enaliarctos* has been variously interpreted as using fore- and hindlimbs and the axial skeleton in swimming⁹ or as being a hindlimb-dominated swimmer²⁴.

The discovery of *Puijila* and the results of the phylogenetic analysis presented here support the hypothesis that pinnipeds diverged from an arctoid ancestral population by the early Oligocene. The non-marine pinniped *Potamotherium* was present in mid-latitudes of Europe and North America, and is known from the Oligocene/Miocene boundary through to the end of the Miocene^{25,26}. *Puijila* itself appears to be a relict stem pinniped. It is the least aquatically specialized of all known pinnipeds (except possibly *Amphicticeps*, for which postcrania are unknown), yet it appears in the fossil record in the early Miocene, approximately contemporaneously with the more highly derived pinniped *Enaliarctos*, and not long before a significant radiation of other early marine pinnipeds¹⁵.

Puijila and *Potamotherium* were not marine specialists, but seem instead to have predominantly lived and hunted in fresh water, suggesting a freshwater phase in the evolutionary transition of pinnipeds from land to sea. Another presumed freshwater pinniped is *Semantor*, a form more aquatically specialized than *Potamotherium*, recovered from upper-Miocene cross-bedded sands along the Irtysh River near Pavlodar in northeastern Kazakhstan²⁷.

An Arctic origin for pinnipeds has previously been proposed^{28,29}, but was later dismissed for lack of fossil evidence¹⁵. Evidence of a morphologically primitive Arctic pinniped has now been found. A far-northern centre of distribution is consistent with the occurrence of marine fossil pinnipeds, the oldest of which are currently known from the early Miocene of the North Pacific (*Enaliarctos*) and the late Oligocene of the North Atlantic (phocids¹⁵). *Puijila* lived in a cool temperate environment where the freshwater lakes would have frozen over in the winter. Early Arctic pinniped populations may have frequented marine shore environments more than their more southerly counterparts, because when freshwater access would have been limited by winter ice, the marine realm would still have been open to hunting.

METHODS SUMMARY

The specimen described here was recovered in 2007 and 2008 from surface collection and screening (wet and dry) in an unconsolidated, yellow-brown, dolomitic siltstone over a 7.4-m² area. The bone is fully three-dimensional, although many elements were found as broken pieces. Excluding the ribs, which are poorly preserved, the skeleton is ~65% complete.

Phylogenetic analyses began with a published craniodental data matrix that focused on basal arctoids, including *Amphicticeps*². The emphasis on basal arctoids aims to avoid the effects of long branch attraction. *Hesperocyon* and *Miacis* represent arctoid outgroups². Some characters were modified and some scores for *Potamotherium* were corrected. Four new taxa were added, namely *Puijila*, the pinniped fossil relative; *Enaliarctos*; and the modern musteloids, *Mustela* (weasel) and *Lontra* (river otter). Although it may have been useful to include the semi-aquatic late-Tertiary *Semantor* in the data analysis, this taxon is known from only the posterior part of the skeleton, which could not be expected to contribute to the phylogenetic approach sought here. The data matrix comprised 26 taxa and 42 unordered characters. Parsimony analyses used the PAUP* software (version 4.10b)³⁰. Two heuristic searches were conducted. The first was without any constraint (Fig. 4). In the second, the heuristic search was bounded by a backbone constraint tree that recognizes the relationship, (Ursidae (Musteloidea + Pinnipedia)), supported by molecular evidence^{5,6}. In the constrained search, only trees that satisfy the following relationship were retained: ((*Miacis*, *Hesperocyon*) (*Cephalogale* (*Enaliarctos* (*Ailurus*, *Mustela*, *Lontra*))))). Matrix, character list, specimen list and search results are available in Supplementary Information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions N.R. was field leader and was responsible for phylogenetic analysis and postcranial study; M.R.D. was responsible for craniodental anatomical description and systematic study; R.H.T. was responsible for phylogeny and palaeogeography.

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