

Marine mammal genomes: Important resources for unravelling adaptation and evolution in the marine environment

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WHY STUDY MARINE MAMMALS

Oceans cover more than 71% of Earth's surface, representing our planet's largest contiguous set of habitats. Not only did life begin in water, but the 1.3 billion cubic kilometers of seawater provides around 300 times more habitable volume than terrestrial environments. Studying marine creatures is of vital importance for investigating evolutionary processes and global biodiversity. Marine mammals can broadly be defined as mammals whose terrestrial predecessors entered the sea and obtain all or most of their food from a marine environment. They are the top predators in the ocean, and play important roles in marine ecosystems. The 129 extant marine mammal

species can be divided into three orders representing multiple independent reversions to the marine environment: (i) Cetaceans diverged from their most recent common ancestor (MRCA) with Artiodactyls approximately 55.5 million years ago (Mya), (ii) pinnipeds and polar bears diverged from their Carnivoran MRCA around 27.4 Mya and 400,000 years ago respectively, and (iii) sirenians split from their MRCA with terrestrial proboscids in the region of 63.9 Mya.¹ It is postulated that marine mammal adaptation strategies were driven by the creation of novel niches as the result of environmental and climate change (Figure 1).

With new genome sequencing and population resequencing techniques,

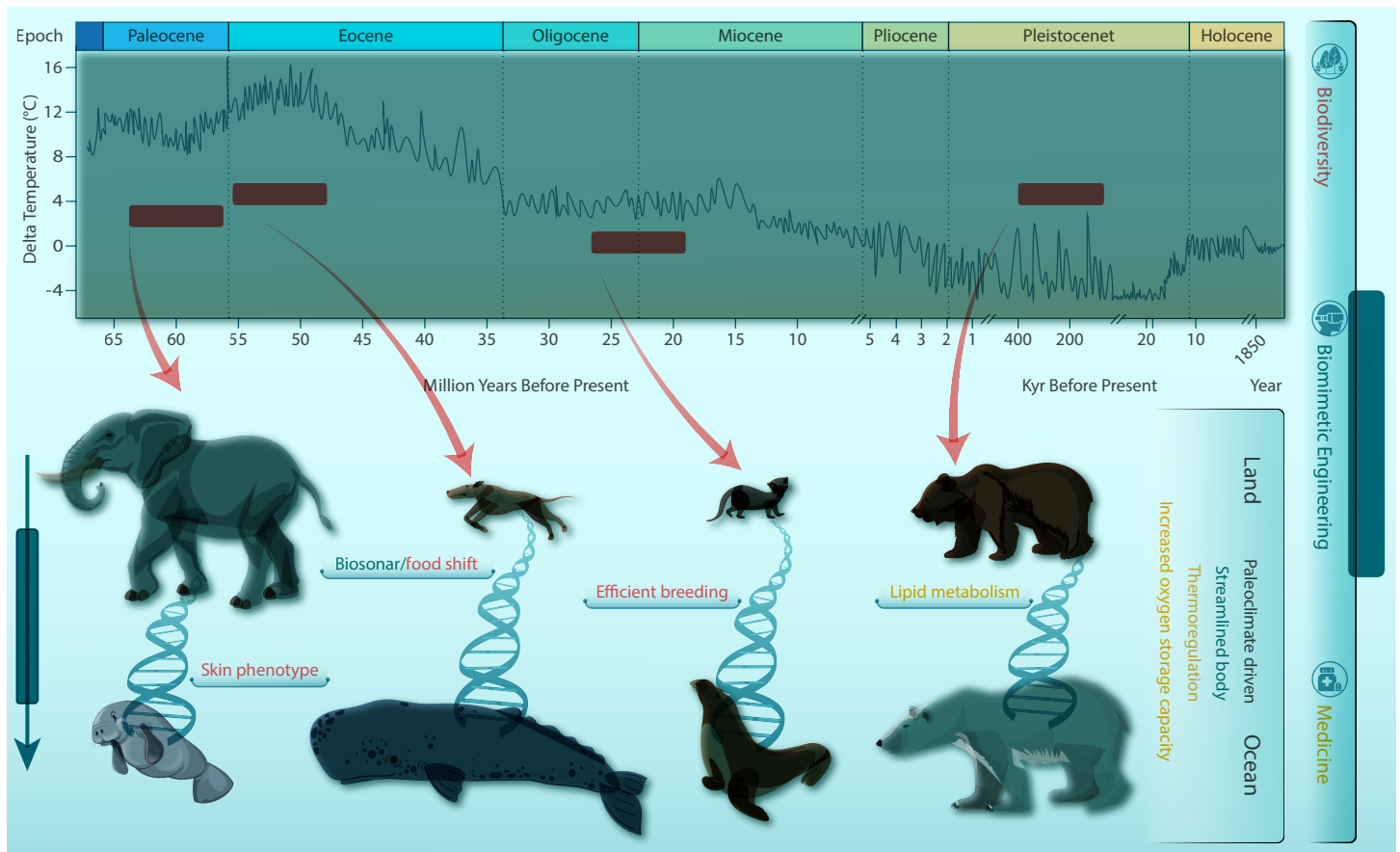


Figure 1. Origin and evolution of marine mammals

we are now uncovering the evolutionary histories and environmental adaptation strategies of many animal systems in incredible detail, from the origin and evolution of tetrapods, to birds and polar bears. Primates are a striking example of an adaptative radiation among terrestrial mammals. The recent culmination of a massive sequencing effort for the order, covering 233 species (representing 86% of genera and all 16 families), reveals their evolu-

tionary history with exceptional resolution, and comparisons across species are set to provide deep insights into the basis of phenotypic variation and will also progress our understanding of human biology and disease. Through the primate genome project, numerous common and rare genetic variants have been identified. Considering the possibility that variants in non-human primates may have similar effects to those in humans, utilizing non-human

primate variants can provide valuable insights for predicting human disease risk.²

Genome projects for marine mammals are similarly vital to reveal the origin, adaptation, radiation, and diversification of these species. However, to date, marine mammal genome projects have been limited by sampling, and there is a long way to go to unlock the potential of this group as model systems to understand mammalian phenotypic, physiological and behavioral adaptations to marine environments. Inference of past responses to climate variation and the prediction of future impacts of environmental change are also possible from genome scale data. Given their role as top predators, evaluating how marine mammal populations will respond to climate change is a priority for understanding the future structure and functioning of marine ecosystems.

WHAT CAN WE LEARN FROM MARINE MAMMALS

Throughout geological time, environmental and climate change have been the main factors driving animal evolution and speciation. The divergence of sirenians from their MRCA with terrestrial proboscids 63.9 Mya coincides with the major mass extinction event of the Latest Danian Event (LDE), which caused the extinction of the dinosaurs. The origin of cetaceans matches the Paleocene-Eocene Thermal Maximum 55 Mya, the appearance of the first baleen whales follows the onset of Oligocene global cooling 33 Mya and expansion of polar sea ice. Pinnipeds evolved during the middle Oligocene when Drake Passage opened, and large carnivores diversified globally.¹ Polar bears are a particularly unique species that quickly adapted to the polar environment due to the MIS11 warm period and following environmental collapse that occurred approximately 400,000 years ago. Genome scale analyses of polar bears have revealed that multiple introgression events and significant gene flow from sister lineages of brown bear, are a key feature of their evolutionary history.³

As fully aquatic (*i.e.* cetaceans and sirenians) or semi-aquatic (*i.e.* pinnipeds) species, marine mammals have evolved unique traits to support life in the ocean, spanning morphological, sensory, physiological and behavioral adaptations. For example, they have developed streamlined body shapes to facilitate movement through the water, increased oxygen storage capacity in body tissues and tolerance of hypoxia for diving, thermal insulation mechanisms, and more. Baleen whales have evolved feeding strategies that have allowed them to achieve the largest body sizes of any animal group in the history of life on Earth, while toothed whales have evolved biosonar systems for navigation and hunting in the water. Pinnipeds, have evolved highly specialized breeding strategies, such as embryonic diapause, and the spatial and temporal separation of foraging from pup rearing, which is underpinned by the ability to store energy in blubber, and provision of fat rich milk. Hooded seals, which breed on unstable Arctic pack ice, have the shortest lactation period at just four days, and highest milk fat content of any mammal, making them the most efficient nursing species in the world. Other marine mammal adaptations include longevity, and cancer resistance. Some details are shown in Figure 1.

These marine mammal characteristics provide crucial insights for understanding environmental, ecological and evolutionary processes influencing mammalian biodiversity. Moreover, such knowledge has important practical applications, for example studying the streamlined body shapes and echolocation that have evolved in marine mammals for efficient movement and navigation in water have direct applications in biomimetic engineering. One example being designs for more efficient wind turbine blades that mimic the foreflippers of humpback whales. In medicine, research on marine mammal thermoregulation, longevity, cancer resistance, hypoxia tolerance and lipid metabolism could lead to breakthroughs in human health,^{3,4} by giving insights into the molecular basis of physiological systems that could be future thera-

peutic targets relevant to aging, obesity, diabetes, heart disease and stroke recovery.^{3,4} Further, a deeper understanding of the molecular basis of marine mammal adaptations will also contribute to the development of more effective conservation plans for these species.^{3,5}

CURRENT KNOWLEDGE AND FUTURE PERSPECTIVE

Although the origin and phylogeny of marine mammals are reasonably well understood, how climate, environmental and ecological changes drove their speciation and diversity remains largely unknown. Marine mammals are widely distributed around the world, from shallow to deep ocean waters (up to 3000 meters), from coastal to pelagic zones, and from tropical to polar regions. However, studying marine mammals is challenging due to their inaccessibility in their natural habitats, making the collection of material for genome sequencing a considerable undertaking for some species.

Studies employing relatively small numbers of the first genomes available across all marine mammal groups have identified notable molecular convergent evolution, providing insights into fundamental biophysical processes such as echolocation, thermoregulation, diving physiology, and fundamental molecular evolutionary theory with the relationship between adaptive molecular convergence and phenotypic convergence.¹ Several population-based genomic work have also been conducted in some cetacean species to elucidate their demography, speciation, and molecular adaptation in different geographic populations.⁵ For example, finless porpoises, Indo-Pacific humpback dolphins, bottlenose dolphins, and Indo-Pacific bottlenose dolphins.

In recent years, the establishment of an international collaborative effort, The Pinniped Genomes Consortium, has brought together scientists for a shared purpose. This network aims to: 1) unite global researchers with diverse expertise in pinniped research; 2) complete chromosome scale reference genomes for pinniped species; 3) facilitate the exchange of data and expertise to support collaborative studies on phylogenomics, population history, and functional genomics; and 4) initiate the development of novel methods to integrate functional genomics, physiology, and paleoenvironment data to determine the molecular basis of pinniped adaptations and their evolutionary history in relation to paleoenvironmental changes. Marine mammal genomics is now entering a new and ambitious phase, similar to the bird and primate genome initiatives. Marine mammal genomes will contribute unique and significant insights into our understanding of mammal evolution, adaptation, disease, conservation, and future prospects in an era of climate change.

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DECLARATION OF INTERESTS

The authors declare no competing interests.