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Exploration of marine mammal paleogeography in the Northern Hemisphere over the Cenozoic using beta diversity

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ABSTRACT

Previous studies on fossil marine mammal biogeography have identified several key geographical routes hypothesized to play a prominent role in their dispersal. This study aims to assess the degree to which each route plays a role. Data on fossil marine mammal temporal and geographic distributions were derived from the Paleobiology Database. We used a beta diversity metric, the Sørensen–Dice coefficient, to measure faunal similarity across ocean basins over the Cenozoic. Faunal similarity was high between the Mediterranean and the Atlantic but relatively low between the Mediterranean and the Pacific. Faunal similarity was observed across both halves of the North Pacific for all four groups in this study. Modern high similarity values between the Atlantic and the Pacific were not observed in the fossil record and were established in the Quaternary. The Strait of Gibraltar is shown to be a pivotal passageway for the dispersal of marine mammals, first in the Eocene as sirenians and cetaceans leave the Tethys Sea, and again as marine mammals reinvade the Mediterranean following the Messinian Salinity Crisis. The Central American Seaway plays only a minor role in marine mammal dispersal. Modern faunal similarity is the result of recent dispersal events in the Quaternary through the Arctic Ocean.

1. Introduction

Mammals have returned to a predominantly marine lifestyle in at least seven separate instances: *Ursus maritimus* (polar bears), marine mustelids (sea otters), *Thalassocnus* (extinct marine sloths), Desmostylia (extinct tethytherian or perissodactyl herbivores), Sirenia (manatees and dugongs), Pinnipedimorpha (seals, sea lions, and walruses), and Cetacea (whales, dolphins, and porpoises). The return to a marine environment has prompted notable changes in skeletal and soft tissue morphology that have facilitated a marine lifestyle (Uhen, 2007). Of these taxa, sea otters, polar bears, and *Thalassocnus* exhibit fewer (if any) skeletal changes in morphology easily noted in the fossil record (Uhen, 2007). The Paleobiology Database contains 25 occurrences of *U. maritimus*, 32 occurrences of marine mustelids, and 8 occurrences of *Thalassocnus* (Table S1, Appendix S1; supplementary material). Based on the low number of fossils and the low diversity of each group, the three taxa were subsequently excluded from the remainder of this study.

1.1. Desmostylia

Desmostylia are semi-aquatic herbivorous marine mammals endemic to the North Pacific and thought to be related to Sirenia and Proboscidea. Desmostylia was placed within the newly named Tethytheria along with Sirenia, Proboscidea, and Embrithopoda (McKenna, 1975). Recently, this relationship has been called into question. A phylogenetic analysis undertaken to reassess the relationships of Anthracobunidae consistently placed Desmostylia as stem perissodactyls (Cooper et al., 2014), suggesting that the relationship between Afrotheria and Perrisodactyla is still not well understood (Rose et al., 2014). Desmostylia first appear in the fossil record in the Rupelian (Early Oligocene) of Oregon and Washington, persist through the Tortonian (Late Miocene), and remain restricted to the margins of the North Pacific Ocean (Barnes, 2013; Beatty, 2009). This would suggest a Northeast Pacific origin, although both the oldest perissodactyls and tethytherians are from the Old World. Regardless, dispersal along the Aleutian–Kamchatka archipelago quickly results in a trans-Pacific distribution for desmostylians.

1.2. Sirenia

Sirenia are herbivorous marine mammals that include manatees and dugongs. There are four extant species (three in the manatee genus *Trichechus* and one in the dugong genus *Dugong*), although a fifth (*Hydrodamalis gigas*) was extant as recently as the eighteenth century before being driven to extinction by human hunting (Domning, 1978).

Sirenia are members of Tethytheria along with Proboscidea, Embrithopoda, and perhaps Desmostylia (McKenna, 1975; but see Cooper et al., 2014). While their closest relatives (proboscideans) were all known from around the Tethys Sea, the earliest sirenians are

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known from the Ypresian of Jamaica (Savage et al., 1994). This discrepancy between the place of origin of these sister taxa was somewhat mitigated by the discovery of a prorastomid from the Lutetian of Senegal (Hautier et al., 2012), and an even more primitive sirenian from the Ypresian or Lutetian of Tunisia (Benoit et al., 2013), confirming that early Eocene sirenians inhabited the Old World as well as the New World. One hypothesis regarding sirenians' dispersal to the New World suggests that they followed the quasi-continuous shoreline from Europe to North America, similar to Eocene land mammals (Geisler et al., 2005; Hautier et al., 2012; McKenna, 1975). This implies that semi-aquatic sirenians would not have needed to cross deep water. Hautier et al. (2012) also suggest an alternate hypothesis: a direct transatlantic dispersal from West Africa to the Americas, similar to that put forth for whales by Uhen (1999).

In the Early Miocene, Caribbean sirenians used the Central American Seaway (CAS) to colonize the sheltered coasts of California and were subsequently isolated, first by an ecological barrier northwest of the seaway termed the "Mexican barrier" and then by the closure of the seaway in the Pliocene (Domning, 1976, 1978). In the Pleistocene, Atlantic manatees dispersed to Africa and replaced the remaining eastern Atlantic dugongs in the fossil record (Domning, 1982, 2005). In the Pacific, hydrodamalines became the only known sirenians to adapt to cold-water environments, and dispersed north and around the Aleutian–Kamchatka archipelago to the Northwest Pacific (Domning, 1976, 1978). The last of these, *Hydrodamalis*, was hunted to extinction in the 18th century (Domning, 1978).

1.3. Pinnipedimorpha

Pinnipedimorpha is a monophyletic group within Caniformia within Carnivora. Pinnipedimorpha includes three clades: Otariidae (fur seals and sea lions), Phocidae (true seals), and Odobenidae (walruses), and several stem taxa (Deméré et al., 2003; Repenning et al., 1979). The first well-documented pinnipedimorphs are Late Oligocene (Berta et al., 1989). A specimen claimed to represent an Eocene phocid (Diedrich, 2011) is highly dubious and is not considered here.

Two femora from the Oligocene of South Carolina have been identified as phocids but share traits with the otters *Enhydra* and *Lutra* (Koretsky, 2002a). Here, we regard them as indeterminate carnivorans; they share an equal number of traits with phocids and mustelids. Similarly, an early Miocene fossil from Devon Island, Canada, *Puijila darwini*, was originally described as a basal pinniped (Rybczynski et al., 2009) but was reidentified as a mustelid (Koretsky and Domning, 2014).

It has been suggested that these specimens, in conjunction with another questionable old world fossil from the Miocene of the Tethys (Koretsky, 2002b), may point to polyphyletic origin of Pinnipedimorpha with an Atlantic origin for Phocidae (Koretsky, 2002a; Koretsky and Barnes, 2006). This diphyletic origin has gained little support in the literature and is largely inconsistent with molecular evidence (Arnason et al., 2006; Arnason and Widegren, 1986; Berta and Wyss, 1994; Dasmahapatra et al., 2009; Fulton and Strobeck, 2010).

The oldest fossils that can be confidently attributed to Pinnipedimorpha are those of *Enaliarctos*, from the Late Oligocene of California (Berta et al., 1989). Pinnipedimorpha were thought to have been restricted to the North Pacific during the Early Miocene when the three major groups arose before individually dispersing out of the North Pacific (Deméré et al., 2003).

1.4. Cetacea

Cetacea are marine mammals that are most closely related to Hippopotamidae within Artiodactyla (Uhen, 2010). The oldest cetacean is either *Himalayacetus* or *Pakicetus*; either indicates a Ypresian origin in the Tethys Sea (Bajpai and Gingerich, 1998; Gingerich and Russell, 1981). In the Early Eocene, only these earliest whales, in the family Pakicetidae, were present and they had not yet left the Tethys Sea. During the Middle Eocene, the more derived archaeocetes, Protocetidae and Basilosauridae, dispersed out of the Tethys and reached Northern Europe, West Africa, and the Americas (Uhen, 2010). Basilosauridae include the first fully aquatic cetaceans, and are the earliest known to have extended their range into the Southern Ocean (Köhler and Fordyce, 1997). They are also the only archaeocete family that survived to the Late Eocene (Uhen, 2010).

Around the Eocene–Oligocene boundary, the cetacean fauna transitions from archaeocetes to Neoceti, which includes the two extant cetacean suborders, Mysticeti and Odontoceti. This transition is poorly understood because the fossil record at the Eocene–Oligocene boundary is sparse (Uhen and Pyenson, 2007). Neoceti are derived from Basilosauridae and each suborder is presumed monophyletic (Uhen, 2007, 2010).

The oldest fossil neocete is the mysticete *Llanocetus* from the latest Eocene of Antarctica (Mitchell, 1989), although by the Oligocene they are found throughout most of the Pacific (Fitzgerald, 2010) as well as the eastern United States (Sanders and Barnes, 2002). Odontocetes appear in the fossil record quite suddenly in the Rupelian in both the Pacific and the Atlantic (Uhen, 2008). The diversification and subsequent dispersal of both Odontoceti and Mysticeti are too sudden to be properly captured by the relatively poor fossil record of the Eocene–Oligocene boundary (Uhen, 2010).

1.5. Biogeographic Processes

Evaluating vicariance in the fossil record of marine vertebrates has proven difficult, and few large-scale studies have been conducted on the subject. Allmon (2001) suggested that vicariance is difficult to assess due to the incompleteness of the fossil record and noted that most documented cases of vicariance in the marine record pertain to invertebrates, in part because marine invertebrates often have smaller ranges and an abundant fossil record when compared to marine vertebrates.

Some authors (Davies, 1963; White, 1986) have suggested the distribution of modern marine mammals have been heavily influenced by vicariance following the end of the Pleistocene. These authors speculate that cold-water-adapted cetaceans followed the cold climates as they receded towards the poles at the end of the Pleistocene, resulting in an antitropical distribution of many cetaceans, where geminate sister species inhabit temperate and/or polar regions in the northern and southern hemisphere, but are isolated by the tropical waters at the equator.

Unfortunately, the paucity of the marine mammal fossil record in the southern hemisphere restricted our study to the northern hemisphere and prevented us from assessing the geminate species hypothesis. More recently, Bisconti (2014) proposed several vicariance events for a family of cetotheres, but speculated only briefly on the geographic cause of the vicariance.

In this study, we interpret the biogeography of marine mammals to be primarily the result of dispersal. Only two major geographic events capable of causing vicariance between ocean basins occur in the Cenozoic: the closing of the Strait of Gibraltar at the end of the Miocene and the raising of the Isthmus of Panama in the Pliocene. The Strait of Gibraltar closure is paired with a major desiccation event (see Sections 1.5.1. and 3.2.2); any speciation as a result of vicariance is masked by high rates of local extinction. The low similarity values before the closure of the Isthmus of Panama (Section 3.3) indicate that few taxa were isolated by its emergence. We thus conclude that vicariance is of little or no consequence to the distributions of marine mammals within the northern hemisphere.

1.5.1. The Strait of Gibraltar

The Strait of Gibraltar may well have served as a critical dispersal route for marine mammals, as Cetacea (and conceivably Sirenia) could have left the Tethys Sea through the Strait of Gibraltar into the Atlantic Ocean (Uhen, 1999; Uhen et al., 2011). This hypothesis bears testing, as