# Evolution of Mammalian Diving Capacity Traced by Myoglobin Net Surface Charge

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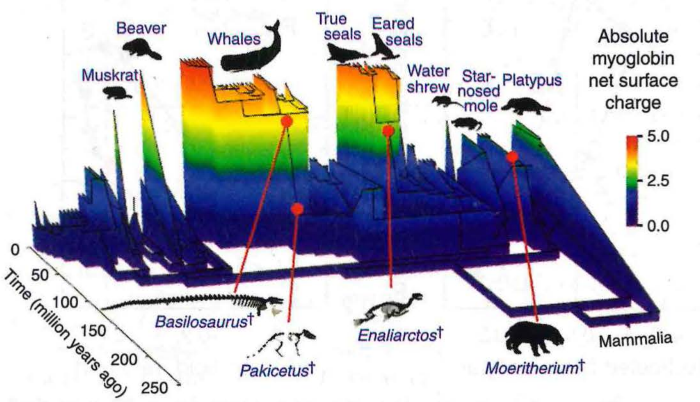
**Introduction:** Evolution of extended breath-hold endurance enables the exploitation of the aquatic niche by numerous mammalian lineages and is accomplished by elevated body oxygen stores and morphological and physiological adaptations that promote their economical use. High muscle myoglobin concentrations in particular are mechanistically linked with an extended dive capacity phenotype, yet little is known regarding the molecular and biochemical underpinnings of this key specialization. We modeled the evolutionary history of this respiratory pigment over 200 million years of mammalian evolution to elucidate the development of maximal diving capacity during the major mammalian land-to-water transitions.

**Methods:** We first determined the relationship between maximum myoglobin concentration and its sequence-derived net surface charge across living mammalian taxa. By using ancestral sequence reconstruction, we then traced myoglobin net surface charge across a 130-species phylogeny to infer ancestral myoglobin muscle concentrations. Last, we estimated maximum dive time in extinct transitional species on the basis of the relationship of this variable with muscle myoglobin concentration and body mass in extant diving mammals.

**Results:** We reveal an adaptive molecular signature of elevated myoglobin net surface charge in all lineages of mammalian divers with an extended aquatic history—from 16-g water shrews to 80,000-kg whales—that correlates with exponential increases in muscle myoglobin concentrations. Integration of this data with body mass predicts 82% of maximal dive-time variation across all degrees of diving ability in living mammals.

**Discussion:** We suggest that the convergent evolution of high myoglobin net surface charge in mammalian divers increases intermolecular electrostatic repulsion, permitting higher muscle oxygen storage capacities without potentially deleterious self-association of the protein. Together with fossil body-mass estimates, our evolutionary reconstruction permits detailed assessments of maximal submergence times and potential foraging ecologies of early transitional ancestors of cetaceans, pinnipeds, and sea cows. Our findings support amphibious ancestries for echidnas, talpid moles, hyraxes, and elephants, thereby not only establishing the earliest land-to-water transition among placental mammals but also providing a new perspective on the evolution of myoglobin, arguably the best-known protein.




**Evolutionary reconstruction of myoglobin net surface charge in terrestrial and aquatic mammals.** The figure reveals a molecular signature of elevated myoglobin net surface charge in all lineages of living elite mammalian divers with an extended aquatic history (upper silhouettes). This signature is used here to infer the diving capacity of extinct species representing stages during mammalian land-to-water transitions (†).

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