## Substitutions in the Glycogenin-1 Gene Are Associated with the Evolution of Endothermy in Sharks and Tunas

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## Abstract

Despite 400–450 million years of independent evolution, a strong phenotypic convergence has occurred between two groups of fish: tunas and lamnid sharks. This convergence is characterized by centralization of red muscle, a distinctive swimming style (stiffened body powered through tail movements) and elevated body temperature (endothermy). Furthermore, both groups demonstrate elevated white muscle metabolic capacities. All these traits are unusual in fish and more likely evolved to support their fast-swimming, pelagic, predatory behavior. Here, we tested the hypothesis that their convergent evolution was driven by selection on a set of metabolic genes. We sequenced white muscle transcriptomes of six tuna, one mackerel, and three shark species, and supplemented this data set with previously published RNA-seq data. Using 26 species in total (including 7,032 tuna genes plus 1,719 shark genes), we constructed phylogenetic trees and carried out maximum-likelihood analyses of gene selection. We inferred several genes relating to metabolism to be under selection. We also found that the same one gene, glycogenin-1, evolved under positive selection independently in tunas and lamnid sharks, providing evidence of convergent selective pressures at gene level possibly underlying shared phylosology.

Key words: tuna, sharks, endothermy, positive selection, phylogenetics.

## Introduction

Bony fishes and sharks have been separated by up to 450 million years of independent evolution (Venkatesh et al. 2014). As such they differ in many aspects of their physiology, anatomy, and biochemistry (Bernal et al. 2001). Despite this, there is remarkable phenotypic convergence between two groups of active, epipelagic predators: the lamnid sharks (= family Lamnidae) and the tunas (= genera *Thunnus*, *Euthynnus*, *Auxis*, and *Katsuwonus* within family Scombridae). These two groups have a distinctive positioning

of red muscle (RM), a specialized swimming style and can warm up regions of body (endothermy).

First, RM is used for slow-twitch contraction, as in steady state swimming. It is primarily fuelled by aerobic metabolism, and as such is relatively rich in mitochondria and myoglobin compared to white muscle (WM). This WM is fast-twitch muscle used for burst swimming, primarily fuelled by glycolysis (anaeroby). As such, WM has lower concentrations of myoglobin and mitochondria (Dickson 1996). Typically, in fish, the majority of RM is located superficially, close to the outside of

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