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The evolution of metabolic regulation in animals

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ABSTRACT

Energy metabolism is determined by a suite of regulatory mechanism, and their increasing complexity over evolutionary time provides the key to understanding the emergence of different metabolic phenotypes. Energy metabolism is at the core of biological processes because all organisms must maintain energy balance against thermodynamic gradients. Energy metabolism is regulated by a bewildering array of interacting molecular mechanisms, and much of what is known about metabolic regulation comes from the medical literature. However, ecology and evolutionary research would gain considerably by incorporating regulatory mechanisms more explicitly in research on topics such as the evolution of endothermy, metabolic plasticity, and energy balance. The purpose of this brief review is to summarise the main regulatory pathways of energy metabolism in animals and their evolutionary origins to make these complex interactions more accessible to researchers from a broad range of backgrounds. Some of the principal regulators of energy balance, such as the AMP-stimulated protein kinase, have an ancient prokaryotic origin. Most regulatory pathways (e.g. thyroid hormone, insulin, adipokines), however, are eukaryotic in origin and diversified substantially in metazoans and vertebrates. Diversification in vertebrates is at least partly due to genome duplications early in this lineage. The interaction between regulatory mechanisms permitted an increasingly sophisticated fine-tuning of energy balance and metabolism. Hence, regulatory complexity increased over evolutionary time, and taxa differ in their potential range of metabolic phenotypes. Choice of model organism therefore becomes important, and bacteria or even invertebrates are not good models for more derived vertebrates. Different metabolic phenotypes and their evolution, such as endothermy and metabolic plasticity, should be interpreted against this regulatory background.

1. Introduction

Energy metabolism is at the core of all life, and an understanding of the differences in metabolic phenotype between individuals, populations, and species is contingent on an appreciation of the diverse mechanisms that regulate metabolism, and their evolution. The aim of this brief review is to provide an overview of these regulatory mechanisms to facilitate a more profound understanding of metabolism in comparative biology. As a first principle, life is governed by the laws of thermodynamics that dictate the direction and rates of biochemical reactions. Maintaining a favourable energy balance is therefore one of the most basic and essential function in all organisms, so that direction and flux through biochemical pathways can be maintained against thermodynamic gradients. All cells must have a constant supply of energy to drive processes that ensure cell integrity, as well as additional energy for reproduction, growth, and activity. The ubiquitous energy storage molecule in all cells is adenosine triphosphate (ATP). Energy from ATP is released by hydrolysis to ADP and AMP (+ phosphates). To maintain energy balance, the various pathways of energy metabolism

must match energy use within the cell with energy available in the environment, and the rate at which environmental energy can be converted into ATP. In animals, most energy is used for protein synthesis and growth, maintenance of ion balance across membranes, activity, and heat production in endotherms (Hulbert and Else, 2000). Environmental energy used by animals is most commonly in the form of ingestible food, and the conversion of food to ATP occurs via metabolic pathways such as glycolysis, and mitochondrial electron transport and oxidative phosphorylation.

All organisms require tight regulation of energy balance, but metabolic regulation becomes more challenging with increasing organismal complexity (Lane and Martin, 2015). Over evolutionary time, ancestral prokaryotic mechanisms of metabolic regulation have diversified, and new mechanisms have evolved which supported the increasing complexity within eukaryotes. Increases in the complexity of prokaryotic organisms may have been constrained energetically. In particular, gene expression and protein synthesis are major components of the energy budget of cells. Eukaryotes may have evolved far greater complexity than prokaryotes because mitochondria provided the

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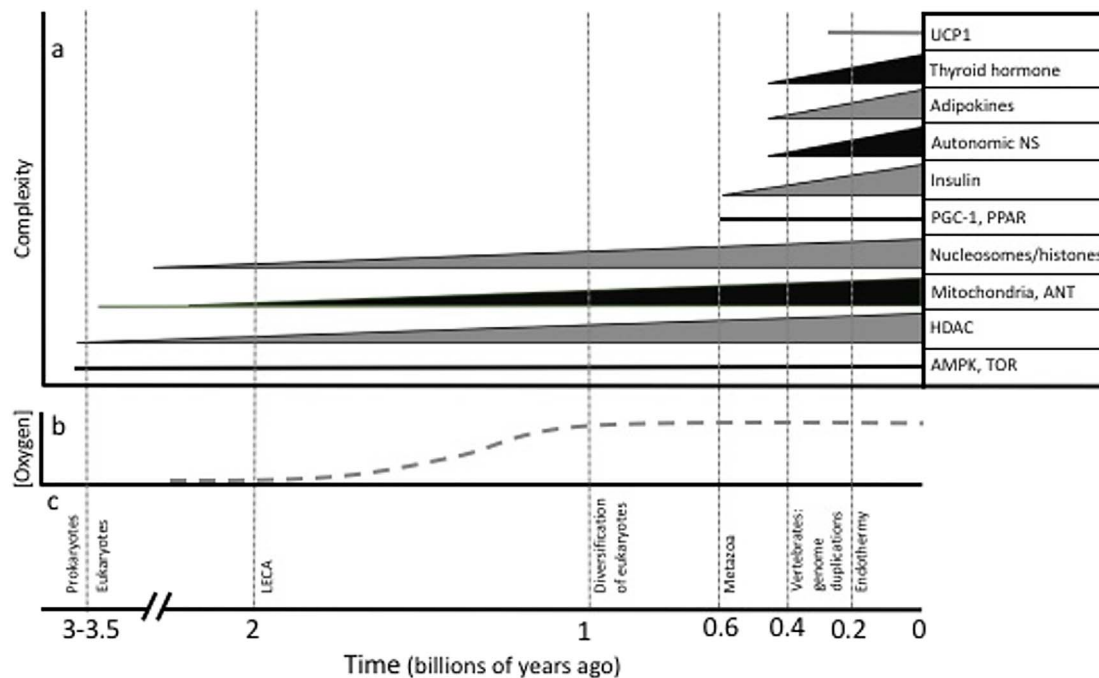


Fig. 1. Summary of major metabolic regulatory systems. The appearance of different mechanisms described in the text (a) over evolutionary time (x-axis) is indicated by the start of the lines corresponding to each mechanisms listed in the right hand column. The increase in complexity of different regulatory systems is indicated by the thickening of the lines into elongated triangles; note that the black and gray shading is for visual clarity only, and that different mechanisms are listed in order of appearance and not complexity. Major evolutionary events are indicated above the x-axis (c), and the approximate timing of increased oxygen concentrations are shown in (b). Note that the time scale is approximate, and more detailed information can be found in the text.

energy necessary to transcribe and translate greater numbers of genes (Lane and Martin, 2010). The greater energetic potential for transcription and translation may have lifted the constraints for selection to favour more complex organisms that required more complex genomes and far greater numbers of expressed genes and proteins (Lane and Martin, 2010). Evolution of metabolism in animals, and particularly increased complexity resulting from genome duplications in vertebrates (Al-Salam and Irwin, 2017; Ross et al., 2016; Van de Peer et al., 2017), resulted in greater regulatory complexity, which is likely to have enabled greater metabolic diversity (e.g. ectothermy and endothermy) and plasticity in response to exercise, diet, and other environmental factors.

Eukaryotes evolved from a prokaryotic ancestor around 3–3.5 billion years ago (Knoll, 2014). During much of their early evolution, the environment was anoxic or hypoxic by modern standards (Lenton et al., 2014) (Fig. 1). A major shift in metabolic organisation of eukaryotes occurred with the integration of mitochondria into eukaryotic cells. Mitochondria were of eubacterial origin and were incorporated into eukaryotic cells by endosymbiosis (Gray et al., 1999). Mitochondria were present already in the last common eukaryotes ancestor (LECA), around 2 billion years ago (Gray et al., 1999; Lenton et al., 2014). At that time, oxygen levels in the oceans remained relatively low, and mitochondria, or mitochondria-derived organelles, functioned anaerobically to a large extent (Muller et al., 2012). Anaerobic mitochondria use endogenously produced terminal electron acceptors such as fumarate or hydrogen rather than oxygen. Today anaerobic mitochondria occur predominantly in organisms that experience low or fluctuating oxygen levels such as intertidal mussels or internal parasites (Muller et al., 2012). Eukaryotes diversified at around 0.8–1 billion years ago (Lenton et al., 2014), which coincided with a substantial increase in environmental oxygen levels (Knoll, 2014) (Fig. 1). Most modern animal cells therefore possess the canonical mitochondria that transform food-derived substrates into biochemically useful energy using oxygen as the terminal electron acceptor. Hence, oxygen consumption has become synonymous with energy metabolism, and oxidative energy

metabolism sustains most activity among animals and it is at the core of the evolution of endothermy.

Measures of metabolic rate have always played a central role in comparative physiology, which reflects the importance of energy metabolism in mediating ecological success and fitness. The energy balance of individuals, and ultimately populations, lies at the core of ecological relationships because it determines flow through trophic cascades. Energetics and metabolism are therefore essential to understanding population dynamics and the effect of environmental change, such as climate change, on population size and persistence. Metabolic rates measured as oxygen consumption are an informative phenotypic measure that is commonly used in the literature (Auer et al., 2017). However, oxygen consumption can be an ambiguous measure of energy metabolism, because a unit of oxygen consumed is not necessarily proportional to a unit of ATP produced (Brand, 2005; Salin et al., 2015). Metabolic rate measured as gas exchange (oxygen consumption or CO₂ production) also has only low resolution in terms of understanding the biological systems that are important in determining energy balance. Whole-organism measures of gas exchange integrate different physiological systems, such as cardiovascular and mitochondrial function without revealing their relative contributions or constraints. Similarly, different regulatory systems may make different relative contributions in determining energy metabolism across individuals, populations, or species. Hence, simple measures of gas exchange are relatively coarse-grained and cannot reveal why organisms are different. Most of the published data on regulatory systems of energy metabolism stem from medical studies using a limited number of model organisms. Hence, there is a need for comparative studies to move beyond oxygen consumption and embrace molecular regulation both to test the generality of insights gained from medical models, and to understand differences between natural populations.

There is a wealth of literature and reviews on regulatory mechanisms of metabolism (e.g. Debevec, 2017; Little, 2016; Towler and Hardie, 2007). My purpose here is not to replicate these reviews, but to provide an overview of how different regulatory mechanisms link

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