

Phylogenetic analysis of the allometry of metabolic rate and mitochondrial basal proton leak

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ABSTRACT

The mitochondrial basal proton leak (MBPL) significantly contributes to high body temperatures (T_b) and basal metabolic rates (BMR) in endotherms. In endotherms at a given body mass (M), liver MBPL is higher than in ectotherms, supporting the notion that MBPL may partly explain the evolutionary increase in metabolic rate (MR), fostering endothermy. Here, we re-addressed this assumption by performing a phylogenetic analysis comparing all available liver MBPL data for ecto- and endotherms. While MBPL within endotherms negatively scales with M and BMR as shown previously, MBPL of ectotherms does not scale allometrically with M . Phylogenetic analysis reveals that this result is confounded by a positive scaling coefficient for MBPL with M for reptiles. Strikingly, the reptilian MBPL reaches endothermic levels above a body mass of 6.6 kg. Thus, phylogenetic scaling of MBPL supports previous claims of endotherm-like physiological characteristics in large reptiles. It appears that diversification of ancestral ectothermic tetrapods to a body mass of at least 6 kg may have been required to reach a MBPL that is beneficial for sustained high body temperatures. Novel MBPL data for the lesser hedgehog tenrec, a protoendothermic eutherian that displays reptile-like thermoregulatory patterns, fall within the endo- and ectothermic allometric regressions. Finally, we add additional evidence that within endotherms, phylogenetic differences in MR do not correlate with MBPL. Collectively, these data suggest that MBPL does not universally scale with metabolic rate in ecto- or endotherms and that an increasing MBPL with M may have played an important physiological role in the evolutionary history of reptilian thermoregulation.

1. Introduction

The mitochondrial basal proton leak (MBPL, $\text{nmol H}^+ \text{min}^{-1} \text{mg protein}^{-1}$) is a result of the inherent leakiness of the mitochondrial inner membrane for protons (Brand et al., 1994a). Consequently, the proton gradient across the mitochondrial inner membrane, storing the energy to form ATP, is partly dissipated as heat. The study of the relationship between MBPL, body mass (M , g) and metabolic rate, defined as the rate of oxygen consumption (MR, $\text{ml O}_2 \text{h}^{-1}$), has evidenced that MBPL in liver and skeletal muscle mitochondria of endotherms significantly contributes to high MRs in endotherms (Brand et al., 1994b; Rolfe and Brown, 1997). The positive correlation of whole body MR and M is accompanied by a decrease in the rate of MBPL in the liver of endotherms (Porter and Brand, 1993).

In contrast, body temperature (T_b) and MR of ectotherms is

governed by ambient temperature (T_a) and the relationship between MBPL, MR, T_b and M is less conclusive. Previous comparisons of MBPL between ecto- and endotherms suggested a higher MBPL in endotherms at similar M , proposing a contribution of MBPL to the evolutionary increase in MR leading to endothermy (Brand et al., 1994b). However, a clear phylogenetic pattern could not be verified (Brookes et al., 1998) and MBPL in ectotherms did not show an allometric relationship with M (Hulbert et al., 2002).

Coinciding with this suggestion, MBPL rates in liver mitochondria of crocodylians were surprisingly reported to match those of endothermic rats (Hulbert et al., 2002). Despite not being classified as endotherms, large crocodylians are indeed capable of maintaining higher average daily T_b s when compared to T_a (Seebacher et al., 1999). In recent years, there has been a lively debate surrounding the evolution of thermoregulation in reptiles with some researchers

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proposing evidence for endotherm-like physiological characteristics in extant crocodiles and extinct dinosaurs (Grady et al., 2014; Seymour et al., 2004).

Protoendothermic mammals or “basoendotherms”, display significantly lower T_b s than the majority of eutherian mammals. The T_b of the lesser hedgehog tenrec (*Echinops telfairi*) in thermoneutral conditions for example is $\approx 32^\circ\text{C}$ (Oelkrug et al., 2013). Additionally, *E. telfairi* remains in an “un-heated” mode most of the time, with body temperatures tracking close to ambient temperatures (Lovegrove and Génin, 2008; Oelkrug et al., 2013). Given our previous understanding of the relationship between MBPL and BMR, we would expect that the MBPL of the tenrec is lower than that of eutherian mammals of the same M that display higher T_b s and BMRs.

Recently, we demonstrated that phylogenetic differences in mass-specific BMR within endotherms are not explained by differences in liver MBPL (Polymeropoulos et al., 2012), where marsupials have higher rates of liver MBPL than eutherian mammals, despite having lower T_b s and mass-specific BMRs. This discrepancy challenges the universality of the causative relationship between high MBPLs and MRs and requires careful re-investigation across all taxa, including ectotherms and basoendotherms.

In order to re-assess the relationship between liver MBPL and MR across more taxa and a wide M range and various levels of thermoregulatory ability, we compiled and analysed all available data for MBPL in liver of endo- and ectotherms from the literature. We also add the MBPL from an unpublished study of a protoendothermic mammal as well as two species of fish. Finally, we discuss the significance of the allometry of MBPL and MR in respect to the transition from ecto- to endothermy and potential implications for a function of high MBPL in reptilian thermoregulation.

2. Material and methods

2.1. Data compilation

Published data for liver MBPL, M and MR of 46 species (19 ectotherms, 27 endotherms) widely ranging in body mass (5.5–46500 g in ectotherms, 12.7–150000 g in endotherms) were compiled from peer-reviewed literature and standardised to common units (Supplement S1 & S2). Here, MR refers to basal metabolic rate (BMR) in endotherms and standard metabolic rate (SMR) in ectotherms (Frappell and Butler, 2004). Any data that were not explicitly specified in the text of the publication were extracted from figures and graphs using the data thief software (v. 1.7).

MR data were only compiled for species for which MBPL data were available in the literature to provide the most accurate representation of the relational data. In the case of the blue shark (*Prionace glauca*) the SMR was estimated based on published SMR data for 21 elasmobranch species greatly ranging in M by fitting ordinary least squares regression (OLS) to Q_{10} standardised (20°C) data (Bernal et al., 2012).

The MBPL and MR data were normalised to taxon-specific “physiological” temperatures and to the common temperature (T) of 37°C using taxon-specific Q_{10} coefficients for MR (White et al., 2006) and a Q_{10} of 1.4 for MBPL (Polymeropoulos et al., 2012). Initial relationships of MR and MBPL with changes in M provided in Figs. 1 and 2 were calculated using OLS, dependent on i) thermoregulatory ability (ectotherms vs endotherms) and ii) phylogeny.

2.2. Phylogenetic analysis of MR, MBPL and M

MBPL and MR of different species may not be statistically independent and failing to account for this non-independence can result in increased type I error rates if phylogeny is not accounted for (Harvey and Pagel, 1991). To incorporate phylogenetic information into our analysis, we first constructed a phylogenetic tree (Supplement

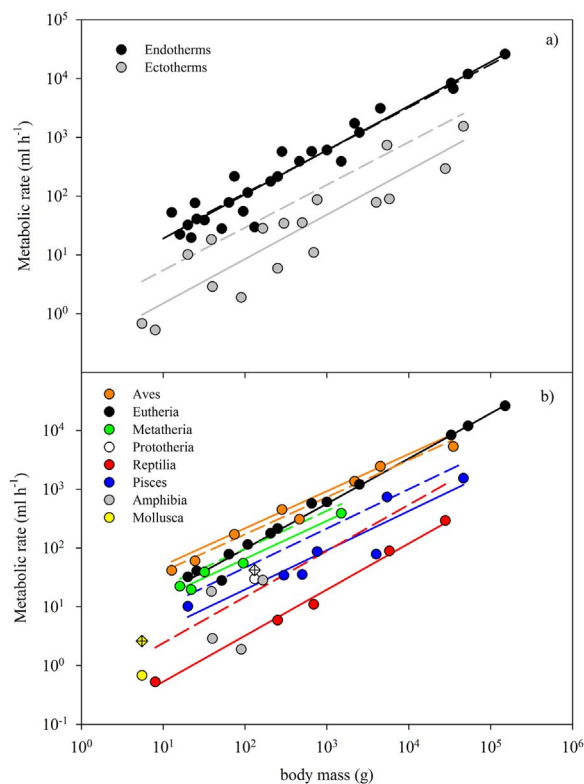


Fig. 1. Allometry of metabolic rate (MR), classified by endo- and ectotherms (a) and separated by phylogeny (b). Dashed linear regressions and diamonds denote Q_{10} extrapolations of metabolic rate data from each group's and taxon's respective body temperature (T_b) to a common temperature of 37°C .

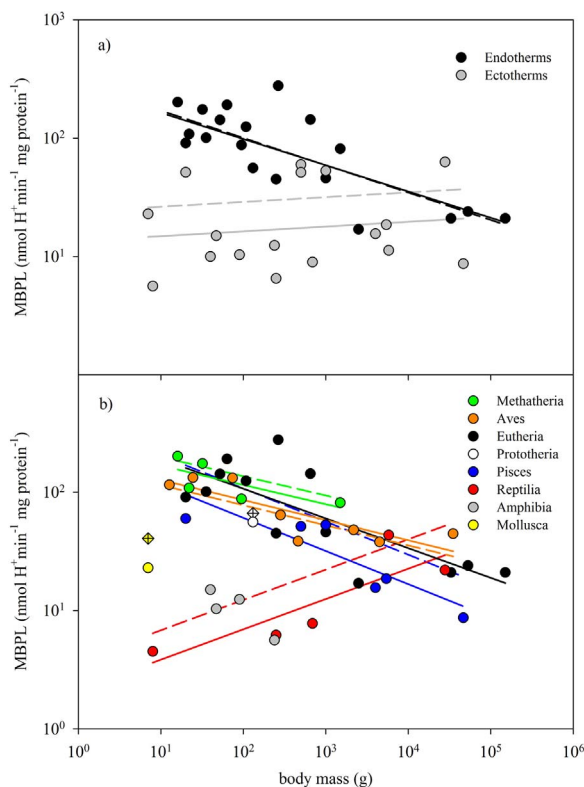


Fig. 2. Allometry of mitochondrial basal proton leak (MBPL) in liver, classified by endo- and ectotherms (a) and separated by phylogeny (b). Dashed linear regressions and diamonds denote Q_{10} extrapolations of MBPL data from each group's and taxon's respective body temperature (T_b) to a common temperature of 37°C . For further details, see Tables 1, 2.

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