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RESEARCH ARTICLE

Evolution of mitochondrial DNA and its relation to basal metabolic rate

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Abstract

Energy metabolism is essential for the survival of animals, which can be characterized by maximum metabolic rate (MMR) and basal metabolic rate (BMR). Because of the crucial roles of mitochondria in energy metabolism, mitochondrial DNA (mtDNA) has been subjected to stronger purifying selection in strongly locomotive than weakly locomotive birds and mammals. Although maximum locomotive speed (an indicator of MMR) showed a negative correlation with the evolutionary rate of mtDNA, it is unclear whether BMR has driven the evolution of mtDNA. Here, we take advantage of the large amount of mtDNA and BMR data in 106 mammals to test whether BMR has influenced the mtDNA evolution. Our results showed that, in addition to the locomotive speed, mammals with higher BMR have subjected to stronger purifying selection on mtDNA than did those with lower BMR. The evolution of mammalian mtDNA has been modified by two levels of energy metabolism, including MMR and BMR. Our study provides a more comprehensive view of mtDNA evolution in relation to energy metabolism.

Keywords

Basal metabolic rate, correlation, energy metabolism, evolution, mitochondrial DNA, selection

History

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Introduction

Energy metabolism is required for the survival of animals, which can be characterized by basal metabolic rate (BMR) and maximum metabolic rate (MMR) (Boratyński & Koteja, 2009). BMR is also termed standard or resting metabolic rate that represents the lowest need of energy at rest, and is taken as the oxygen consumption on unfed, inactive individuals in the dark at temperature under thermoneutral conditions (McNab, 1997). Although BMR is widely applied as an index of energy expenditure of free-living animals (White et al., 2006; White & Seymour, 2003), it can not represent the whole energy expenditure, because BMR and whole energy consumption of an animal do not even have a proportional relationship (Koteja, 1991). In contrast, MMR is the maximum oxygen consumption during the process of exercise when most locomotor muscles are working at their sustainable maximum (Weibel et al., 2004), which is a good indicator of an individual's ability to sustain a high level of locomotor activity and to achieve a high running speed (Henderson et al., 2002; Rezende et al., 2006). BMR and MMR were found to have a positive correlation (Hayes & Garland, 1995; Sadowska et al., 2005) or a weak correlation (Le Galliard et al., 2013), while other authors argued that no correlation between them was observed (Boratyński & Koteja, 2009).

Animal mitochondria generate up to 95% of all the cellular energy production for energy-consuming activities, such as respiration, locomotion and other life activities (Galtier et al., 2009). All the 13 mitochondrial-encoded proteins are essential for energy production, and have been proved to be sensitive to energy-related selective constraints (Castoe et al., 2008; Elson et al., 2004; Shen et al., 2009; Sun et al., 2011; Wang et al., 2011).

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Because of the crucial roles of mitochondria in energy generation and locomotion, a recent study suggested that mitochondrial DNA (mtDNA) has been subjected to relaxed selective constraints in weakly locomotive birds and mammals, and stronger purifying selection in strongly locomotive species (Shen et al., 2009). Although maximum locomotive speed, which can be indicated by MMR (Henderson et al., 2002; Rezende et al., 2006), showed a negative correlation with the evolutionary rate of mtDNA (Shen et al., 2009), it is unclear whether BMR has driven the evolutionary rate of mtDNA. Because BMR indicates the minimum energy demand that is sufficient only for the functioning of the vital organs, which varies considerably across different groups of animals, we hypothesize that mtDNA may have undergone stronger purifying selection in animals with higher BMR. In this study, we take advantage of the large amount of mtDNA and BMR data, both of which are available in a diverse range of mammals. We test whether BMR has driven the evolution of mtDNA in mammals, and provide a more comprehensive view of mtDNA evolution in relation to energy metabolism.

Material and methods

Data sources

Data for BMR and body mass of mammals were culled from previous studies (Bennett & Harvey, 1987; Capellini et al., 2010; McNab, 2008; Müller et al., 2012). Because body mass of mammals varies dramatically, ranging from 10 to 3,221,000 g (Table 1), which significantly affects the energy consumption for basic metabolism (Kleiber, 1947; White & Seymour, 2003, 2005), a body mass-dependent scale is expected to be more stringent and appropriate for characterizing the performance of energy metabolism at rest (Clarke et al., 2010). Therefore, we used ''relative BMR'' (BMR divided by body mass) to normalize BMR across mammals. Furthermore, raw mtDNA sequences of mammals

Table 1. Information of mammals used in this study.

Classification	Number of species	Mass (g)	BMR (kJ/h)
Carnivora	29	77–388,500	5.89–1497.81
Pholidota	2	1430–3637.5	4.59–13.44
Cetartiodactyla	10	20,200–3,221,000	116.82–7826
Chiroptera	2	45.2–363	1.14–4.87
Eulipotyphla	5	10.4–721.2	0.46–10.14
Primates	13	114–60,500	1.55–255.12
Scandentia	1	186	2.54
Lagomorpha	2	109–117.5	2.35–2.82
Rodentia	14	39–250.6	0.52–6.95
Cingulata	1	3320	16
Pilosa	1	3500	17.57
Afrosoricida	2	26.1–34	0.31–0.82
Macroscelidea	1	38.8	1.04
Tubulidentata	1	48,000	123.37
Hyracoidea	2	2210–2400	13.01–15.09
Peramelemorphia	4	837.3–1551	7.11–12.77
Dasyuromorphia	4	17.7–584	0.44–3.73
Diprotodontia	6	10–29300	0.58–111.79
Microbiotheria	1	40	0.64
Didelphimorphia	3	40–336	0.86–4.12

The detailed species information about classification, body mass, basal matobolic rate, references and mtDNA accession number for 108 mammals will be provided on request.

available in January 2012 were downloaded from the GenBank. A total of 106 mammalian species with both mtDNA and BMR data were analyzed. Our dataset contained 20 orders of mammals (Table 1, Figure 1). In addition, the maximum locomotive speed records of mammals were taken from a recent study (Shen et al., 2009).

Phylogenetic reconstruction

All the 13 protein-coding genes were extracted from each mitochondrial genome sequences expect for *ND6*. Because *ND6* is encoded by the other strand of mtDNA with very different codon usage bias (Hasegawa et al., 1998; Wang et al., 2011), we excluded this gene in our analysis. Nucleotide sequences of 12 protein-coding genes were translated into amino acids. Deduced amino acid sequences of each gene were aligned with ClustalX 1.81 (Thompson et al., 1997) and modified by eye with MEGA 5.0 (Tamura et al., 2011). The resultant alignment was the concatenated amino acid sequences of all 12 mitochondrial genes. We used the program ProtTest 2.4 (Abascal et al., 2005) to determine the most appropriate model for the protein evolution and the optimum maximum-likelihood parameters. The maximum-likelihood phylogenetic tree of was reconstructed using PhyML 3.0 (Guindon & Gascuel, 2003) with a Mtmam model as suggested by ProtTest 2.4 (Abascal et al., 2005). The phylogenetic tree (Figure 1) was largely similar to the established species tree (Murphy et al., 2007). In case of conflicts between our mitochondrial gene tree and the species tree, we used the topology from the species tree. When several species within a high

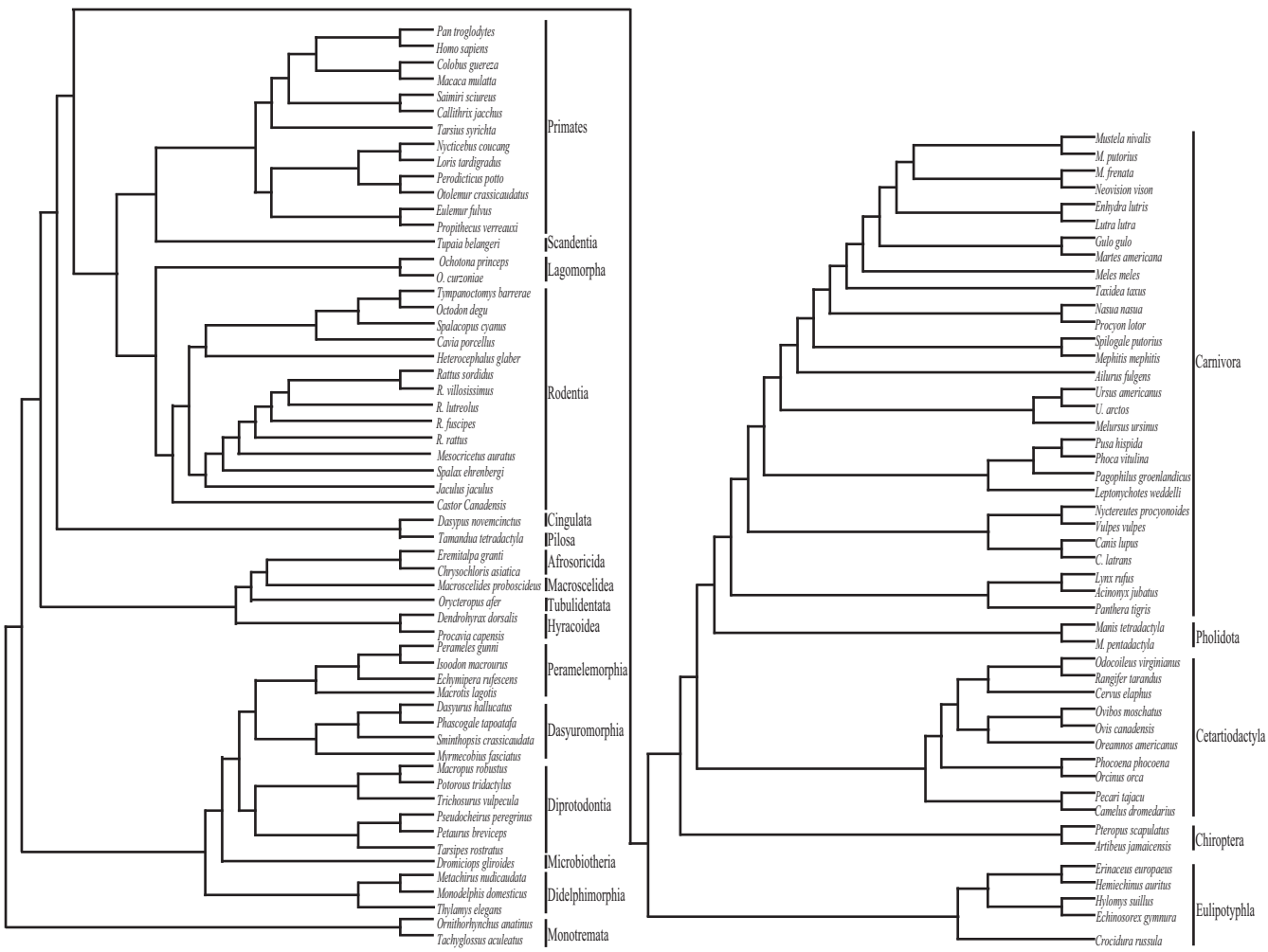

Figure 1. Maximum likelihood phylogenetic tree of 106 mammals reconstructed from mtDNA. A total of 20 mammalian orders are included.

taxonomic rank were unavailable in the species tree, we used the topology recovered from our tree. Of the 106 mamamls, 33 species were shared between this study and a previous study (Shen et al., 2009), a subtree (Figure 2) containing the 33 mammals was extracted from our mitochondrial gene tree.

Molecular evolution

Concatenated amino acid sequences of all 12 mitochondrial genes were translated back to nucleotides. The ratio (Ka/Ks) of nonsynonymous (Ka) to synonymous (Ks) substitution rates was estimated for each branch of the phylogenetic tree using PAML (Yang, 2007). Nonsynonymous substitutions alter amino acid sequences of proteins while synonymous substitutions do not. Ka/Ks ratio is an indicator widely used to measure the strength of natural selection. The input tree for PAML analysis was our mitochondrial gene tree (Figure 1) with modification following the species tree (Murphy et al., 2007). A free-ratio model implemented in PAML was estimated, which assumes an independent Ka/Ks value separately for each branch. Ka, Ks and Ka/Ks values along each terminal branch were compiled for subsequent analyses following a recent study (Shen et al., 2009).

Statistical analysis

To reveal the relationship between BMR and maximum locomotive speed of 33 mammals that are shared in this study and a previous study (Shen et al., 2009), we performed an ordinary linear regression analysis using SPSS 16.0 (SPSS Inc., Chicago, IL). To confirm the potential relationship between BMR and the evolutionary rate of mtDNA, we expanded our dataset to 106 mammals with both available mtDNA sequences and BMR values, and conducted an ordinary linear regression analysis of BMR against Ka, Ks, and Ka/Ks, respectively.

Phylogenetic inertia may affect comparative analyses across a range of species, because more closely-related species tend to share more similar traits (Fisher & Owens, 2004; Harvey & Pagel, 1991). To control the effects of phylogenetic inertia in all ordinary linear regression analyses, we additionally used phylogenetically independent contrasts (Felsenstein, 1985) implemented in Mesquite 2.74 (Maddison & Maddison, 2009) with PDAP module, setting all branch lengths equal. We observed no correlation between the absolute contrast value and standard deviation of all variables ($p = 0.109$, $R = 0.157$), which meets the assumption of independent contrast (Garland et al., 1992).

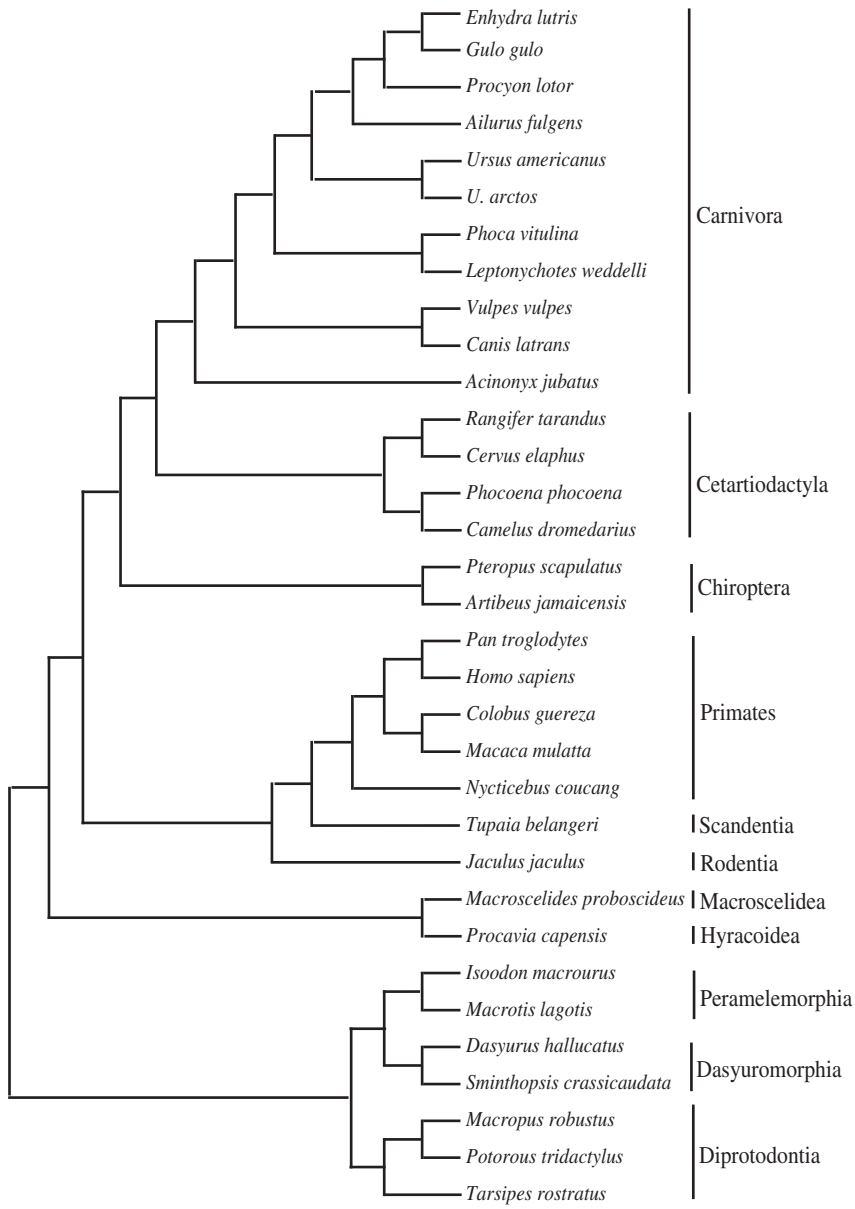

Figure 2. A subset of phylogenetic tree of 33 mammals that are overlapped between this study and a previous study (Shen et al., 2009). A total of 11 mammalian orders are included.

Results

A maximum likelihood phylogenetic tree of 106 mammals was recovered based on 106 complete mitochondrial genomes (Figure 1). Although some branches remain poorly resolved, the overall topology of this tree is consistent to the well-established species tree of mammals based on massive nuclear genes (Murphy et al., 2007). Our dataset of animals contained 20 orders, representing all major orders of mammals (Figure 1).

To examine the association between BMR and the evolution of mtDNA, we first attempted to gain insights by comparing BMR to locomotive speed, because locomotive speed is significantly negatively correlated with Ka/Ks of mtDNA in birds and mammals (Shen et al., 2009). Due to the limited data of birds, we focused on 33 mammals with both BMR and locomotive speed records (Figure 2), this dataset included 11 orders of mammals. We undertook an ordinary linear regression of BMR and maximum locomotive speed for 33 mammalian species. In general, BMR was significantly positively correlated with increasing locomotive speed ($p = 0.011$, $R = 0.438$; Figure 3A), indicating a general pattern for BMR to increase with locomotive speed. Because the 33 mammals had differing phylogenetic affinities, phylogenetic biases might influence our result. We turned to employ Mesquite 2.74 (Maddison & Maddison, 2009) to perform a phylogenetically independent contrast analysis. This analysis showed the same increasing trend in BMR as locomotive speed increases ($p = 0.036$, $R = 0.371$; Figure 3B). Together, both the analyses from the general pattern and phylogeny-based comparison strongly suggested that mammals with higher BMR tend to locomote faster. This finding indicates that BMR may have an increasing trend as Ka/Ks of mtDNA decreases, which is true in the case of locomotive speed (Shen et al., 2009).

To test whether BMR has the same trend as locomotive speed in relation to Ka/Ks variations of mtDNA, we expand our dataset to 103 mammals which have both BMR and mtDNA data. We calculated the Ka/Ks ratio of each species under a free-ratio model and conducted linear regression analyses comparing BMR with Ka/Ks ratio. The average Ka/Ks ratio estimated from the free-ratio model is 0.033, indicative of strong purifying selection and functional constraint, which remove deleterious mutations in mtDNA to maintain high metabolic efficiency in general. In the ordinary regression analysis, we recovered a significant negative correlation between Ka/Ks ratio of mtDNA and BMR ($p = 0.003$, $R = 0.288$; Figure 4A), suggesting a tendency for the Ka/Ks ratio to decrease as BMR increases. In the phylogeny-based regression analysis, we revealed the same decreasing trend in Ka/Ks ratio with BMR, although the correlation is weak ($p = 0.075$, $R = 0.174$; Figure 4B). To avoid the saturation effect of our mtDNA data, we omitted species with synonymous substitution rate (Ks) greater than 2.5, which is a result of saturation (Hutter et al., 2010), and still recovered the same decreasing trend in Ka/Ks ratio with BMR ($p = 0.013$, $R = 0.255$ before controlling for phylogeny; $p = 0.110$, $R = 0.091$ after controlling for phylogeny). Furthermore, we used a lower cut-off and removed species with Ks >2, the similar trend was revealed ($p = 0.009$, $R = 0.268$ before controlling for phylogeny; $p = 0.058$, $R = 0.095$ after controlling for phylogeny). These results suggest that the pattern of the relationship between BMR and Ka/Ks remains largely unchanged after controlling for saturation effect at synonymous sites. Collectively, our results demonstrated that mammals with higher BMR have subjected to stronger purifying selection on mtDNA, to maintain high metabolic efficiency, than did those with lower BMR.

Discussion

Comparative analyses of functional genes provide valuable insights into the relationship between genetics and ecology (Dorus et al., 2004; Zhang et al., 2002; Zhao et al., 2009, 2010). Mitochondria are commonly known as the plant of energy, which provides energy for daily activities including metabolism. Multiple lines of evidence has proven that the evolution of mtDNA has been driven by a number of ecological factors (Castoe et al., 2008; Elson et al., 2004; Mishmar et al., 2003; Sun et al., 2007). Using a comparative approach, a recent study revealed that weakly locomotive animals accumulated more nonsynonymous substitutions in mtDNA than did strongly locomotive species (Shen et al., 2009), although the authors did not consider BMR (the other level of energy metabolism). In this study, we undertook a similar comparative analysis, and discovered that mammals with higher BMR have subjected to stronger purifying selection on mtDNA than did those with lower BMR.

What could potentially have misled our results? Differences in effective population size are unlikely, because the influence of effective population sizes can not fully explain the Ka/Ks variations in birds, mammals and fishes (Shen et al., 2009; Sun et al., 2011). Differences in mutation rate are also unlikely, because we failed to detect a significant linear relationship

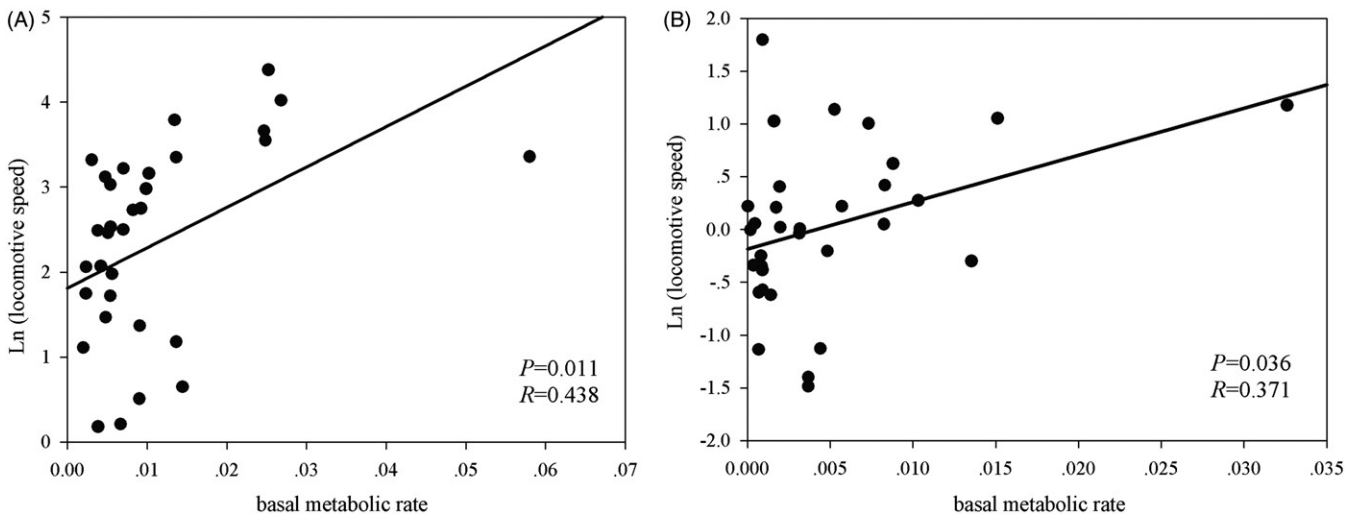

Figure 3. Positive correlation between BMR and maximum locomotive speed in 33 mammals. (A) Ordinary linear regression; (B) Phylogenetically independent linear regression.

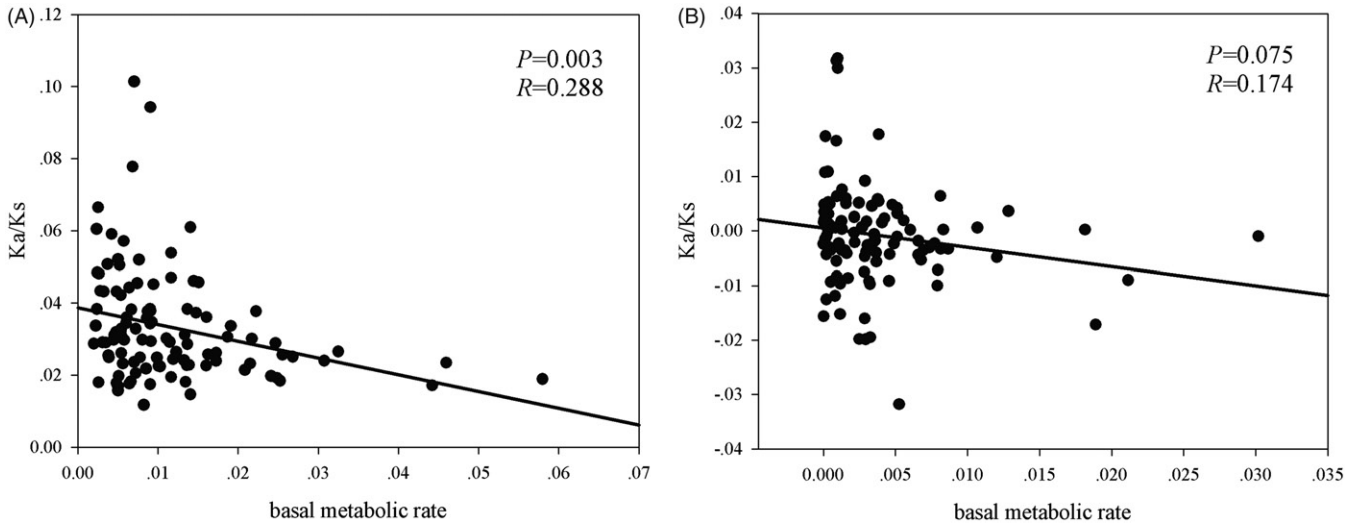

Figure 4. Negative correlation between BMR and mitochondrial Ka/Ks ratios in 106 mammals. (A) Ordinary linear regression; (B) Phylogenetically independent linear regression.

between Ks and BMR ($p = 0.39$, $R^2 = 0.09$). Instead, we observed a decreasing trend in Ka as BMR increases, although it was only nearly significant ($p = 0.09$, $R^2 = 0.27$). This trend suggests that BMR variations play a role in driving the evolution of nonsynonymous rather than synonymous substitutions.

Why do mammals with higher BMR tend to undergo stronger purifying selection on mtDNA than those with lower BMR? Higher BMR requires more efficient energy metabolism, mammals with higher BMR need to maintain high metabolic efficiency of mtDNA to meet their higher demand of energy budget. Hence, these animals cannot tolerate nonsynonymous substitutions that are generally deleterious and potentially cause defects in respiratory-chain activity and other metabolic processes (Wallace, 2005; Weber et al., 1997). In contrast, mammals with lower BMR require lower demand of energy budget, which can tolerate more slightly deleterious mutations. The tolerance may allow for the faster accumulation of more nonsynonymous substitutions in mtDNA as described in domestic animals (Bjornerfeldt et al., 2006; Wang et al., 2011). The efficiency of energy metabolism may have declined in these animals with lower BMR, but they are more readily to survive and reproduce than animals with higher BMR inhabiting similar harsh environments. In addition, similar selection pressure may have influenced additional parts of the genome, the evolution of nuclear genes in relation to energy metabolism should be examined in future (Arnqvist et al., 2010).

Conclusion

In conclusion, in addition to the locomotive speed (an indicator of MMR), mammals with higher BMR have subjected to stronger purifying selection on mtDNA than did those with lower BMR. The evolution of mammalian mtDNA has been modified by two levels of energy metabolism, including MMR and BMR. Our study provides a more comprehensive view of mtDNA evolution in relation to energy metabolism.

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Declaration of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of this article.

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