



Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympevRearrangement and evolution of mitochondrial genomes in parrots [☆]Jessica R. Eberhard ^{a,*}, Timothy F. Wright ^b^a Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA^b Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

ARTICLE INFO

Article history:

Received 11 December 2014

Revised 15 July 2015

Accepted 11 August 2015

Available online 17 August 2015

Keywords:

Mitochondrial genome
Control region duplication
Evolutionary rate
Base composition
Nucleotide skew
Body size effect

ABSTRACT

Mitochondrial genome rearrangements that result in control region duplication have been described for a variety of birds, but the mechanisms leading to their appearance and maintenance remain unclear, and their effect on sequence evolution has not been explored. A recent survey of mitochondrial genomes in the Psittaciformes (parrots) found that control region duplications have arisen independently at least six times across the order. We analyzed complete mitochondrial genome sequences from 20 parrot species, including representatives of each lineage with control region duplications, to document the gene order changes and to examine effects of genome rearrangements on patterns of sequence evolution. The gene order previously reported for *Amazona* parrots was found for four of the six independently derived genome rearrangements, and a previously undescribed gene order was found in *Prioniturus luconensis*, representing a fifth clade with rearranged genomes; the gene order resulting from the remaining rearrangement event could not be confirmed. In all rearranged genomes, two copies of the control region are present and are very similar at the sequence level, while duplicates of the other genes involved in the rearrangement show signs of degeneration or have been lost altogether. We compared rates of sequence evolution in genomes with and without control region duplications and did not find a consistent acceleration or deceleration associated with the duplications. This could be due to the fact that most of the genome rearrangement events in parrots are ancient, and additionally, to an effect of body size on evolutionary rate that we found for mitochondrial but not nuclear sequences. Base composition analyses found that relative to other birds, parrots have unusually strong compositional asymmetry (AT- and GC-skew) in their coding sequences, especially at fourfold degenerate sites. Furthermore, we found higher AT skew in species with control region duplications. One potential cause for this compositional asymmetry is that parrots have unusually slow mtDNA replication. If this is the case, then any replicative advantage provided by having a second control region could result in selection for maintenance of both control regions once duplicated.

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1. Introduction

Mitochondrial DNA (mtDNA) sequence evolution in bilaterian animals is rapid compared with that of nuclear DNA (nucDNA) (Lynch et al., 2006), a feature that has made it useful in phylogenetic reconstruction. In spite of this high rate of sequence evolution, the vertebrate mitochondrial genome was long thought to be relatively stable in terms of genome structure, and rearrangements in gene order were thought to be rare events (Boore, 1999; Gissi et al., 2008). However, over the past 15 years, sequence-based studies have revealed that rearrangements are

not uncommon, particularly in birds, where several different lineages have undergone repeated rearrangements (Abbott et al., 2005; Bensch and Härlid, 2000; Cho et al., 2009; Eberhard et al., 2001; Gibb et al., 2007; Haring et al., 2001; Mindell et al., 1998a; Morris-Pocock et al., 2010; Roques et al., 2004; Schirtzinger et al., 2012; Singh et al., 2008; Slack et al., 2007; Verkuil et al., 2010; Zhou et al., 2014). Despite the growing list of avian taxa in which changes in mitochondrial gene order have been described, questions persist regarding the mechanisms by which rearrangements occur, the degree to which duplications are retained over evolutionary time, and the effect that these rearrangements have on the function, replication, and evolution of the mitochondrial genome.

The mitochondrial genome of most bilaterian animals includes the same set of 37 genes (two ribosomal RNAs, 13 proteins, and 22 tRNAs) and a non-coding control region (Boore, 1999; Lavrov,

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2007). This consistency in gene content across distantly related lineages, as well as the lack of intergenic spacers, suggests that the mitochondrial genome is under selection for compact size (Rand and Harrison, 1986). The first avian mitochondrial genome to be completely sequenced was that of the chicken (Desjardins and Morais, 1990), and its gene order (hereafter referred to as the “typical” avian gene order) is the one most commonly observed in birds. The typical avian gene order differs from most other vertebrates due to a rearrangement near the control region, resulting in the gene order shown in Fig. 1A. In 1998, Mindell et al. reported an alternative avian gene order that contains a non-coding region thought to be a degenerate copy of the control region (Fig. 1H). Subsequently, additional gene orders have been reported for a variety of avian taxa (Table 1), indicating that mitochondrial genome rearrangements are taxonomically widespread and more common than previously thought. Gibb et al. (2007) reviewed the gene orders found in avian mitochondrial genomes and concluded that there are at least four distinct gene orders within birds, with the typical (chicken) gene order being the ancestral one. Since then, another gene order variant has been found in ruffs (Verkuil et al., 2010), and a recent study that examined mitochondrial genome sequences of 16 ardeid birds found four distinct gene orders, including two that had not been previously described, all thought to be derived from a single ancestral genome rearrangement (Zhou et al., 2014). In all cases known to date, the novel avian gene orders can be derived from a tandem duplication of the control region and neighboring genes followed by subsequent degeneration and/or loss of some of the duplicate genes (Bensch and Härlid, 2000) (see Fig. 1 and Table 1).

In most avian taxa that have been examined to date mitochondrial rearrangements involve retention of both duplicated control regions and degeneration of the neighboring duplicated coding

genes (Table 1). Why duplicated control regions are often maintained while neighboring duplicated genes usually degenerate may relate to the function of the control region itself. The control region has long been thought to contain the origin of transcription and replication of the mitochondrial genome (Brown et al., 2005; Shadel and Clayton, 1997), but its precise role in this process is uncertain. In vertebrates, the control region is thought to contain the origin of heavy-strand replication (O_H) and transcription promoters (Clayton, 1982, 1991). However, a study of chicken mtDNA replication concluded that replication of the mitochondrial genome is bidirectional and can initiate across the entire genome, with the majority of initiation events mapping to the ND6 gene, which in the typical bird gene order is just upstream of the control region (Reyes et al., 2005). The Reyes et al. (2005) study re-casts the avian control region as a genomic feature that may function more as a replication promoter (much as a gene promoter initiates transcription of a nearby gene) rather than the replication initiation site itself, as it traditionally has been considered. Given the control region’s involvement in replication, the presence of two control regions could affect rates of evolution in other mitochondrial genes.

One aspect of sequence evolution that could give further insight into the potential role of duplicated control regions is the degree of base composition asymmetry in the DNA strands that compose the mitochondrial genome. In a study of mammalian mtDNA, Reyes et al. (1998) proposed that the asymmetrical base composition (measured as AT and GC skew) is a result of deamination of C and A on the H strand that occurs when the H strand is in a single-stranded state during replication. Species with slower replication would potentially have greater asymmetry because their H strand is in a single-stranded form for longer periods of time. This asymmetry is expected to be strongest at fourfold degenerate sites,

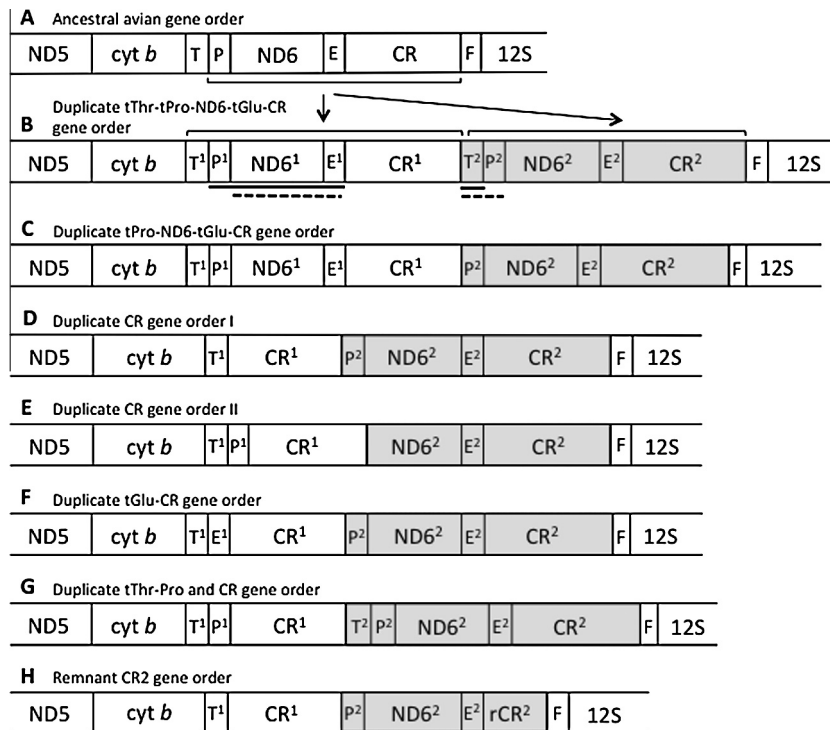


Fig. 1. Gene orders surrounding the control region (CR) known for avian mitochondrial genomes. Brackets and arrows indicate the segment involved in a tandem duplication that has been hypothesized to be involved in the conversion between the standard and alternative gene orders. The solid and dashed lines beneath B indicate sections that degenerate (or are lost) in the transitions from B to D and E, respectively, to yield the two gene orders observed in parrots. Gene order H is similar to D, but the second copy of the control region is degenerate. Transfer RNAs are indicated by their single-letter abbreviations, E (Glutamy), F (Phenylalanine), P (Proline), and T (Threonine). Pseudogenes, which have been described in various taxa for this portion of the mitochondrial genome, are not shown. Shading indicates hypothesized homology between highlighted regions. Taxa for which these different orders have been reported to date are listed in Table 1.

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