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# The *Anolis* Lizard Genome: An Amniote Genome without Isochores?

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## Abstract

Two articles published 5 years ago concluded that the genome of the lizard *Anolis carolinensis* is an amniote genome without isochores. This claim was apparently contradicting previous results on the general presence of an isochore organization in all vertebrate genomes tested (including *Anolis*). In this investigation, we demonstrate that the *Anolis* genome is indeed heterogeneous in base composition, since its macrochromosomes comprise isochores mainly from the L2 and H1 families (a moderately GC-poor and a moderately GC-rich family, respectively), and since the majority of the sequenced microchromosomes consists of H1 isochores. These families are associated with different features of genome structure, including gene density and compositional correlations (e.g., GC3 vs flanking sequence GC and intron GC), as in the case of mammalian and avian genomes. Moreover, the assembled *Anolis* chromosomes have an enormous number of gaps, which could be due to sequencing problems in GC-rich regions of the genome. In conclusion, the *Anolis* genome is no exception to the general rule of an isochore organization in the genomes of vertebrates (and other eukaryotes).

**Key words:** isochores, reptiles, genome structure and evolution.

## Introduction

The discovery of compartmentalization in mammalian genomes goes back to more than 40 years ago when, using $Cs_2$ $SO_4/Ag^+$ ultracentrifugation (Corneo et al. 1968), it was shown that the bovine genome mainly consisted of a small number of families of "main band" (non-satellite, non-ribosomal) DNA molecules 10–20 kb in size (Filipski et al. 1973). This observation was then extended to other eukaryotic genomes (Thiery et al. 1976). The 10–20 kb DNA molecules just mentioned derived, in fact, from much larger DNA stretches, fairly homogeneous in base composition (Macaya et al. 1976), that were called "isochores" for (compositionally) equal landscapes (Cuny et al. 1981; see Bernardi 2004, for a review including later investigations).

The very basic features of isochores are that (1) they belong to a small number of families (five in the human genome: L1, L2, H1, H2, and H3, characterized by increasing GC levels); (2) they are correlated with all structural and functional properties of the genome (such as gene density, replication timing, etc.) that could be tested; (3) they are correlated with the architecture of chromosomes from interphase to metaphase (Bernardi 2015).

Some misunderstandings about isochores (Häring and Kypr 2001; Lander et al. 2001; Belle e al. 2002; Ream et al. 2003; Cohen et al. 2005; Elhaik et al. 2009) were promptly corrected (Bernardi 2001; Clay and Bernardi 2001, 2002, 2005, 2011; Clay et al. 2003; Jabbari et al. 2003). This was not done so far for two articles (Alföldi et al. 2011; Fujita et al. 2011) that claimed that the *Anolis* lizard genome was an amniote genome without isochores. The reason why we did not react quickly to this new misunderstanding was the lack of credibility of this conclusion (which, incidentally, was based on a genome sequence with an enormous number of gaps). Indeed (1) we had shown that an isochores organization was general for vertebrates (Costantini et al. 2009) and that the isochore families present in the genomes studied were very close in terms of base composition (maxima and minima), the only possible difference being the relative amounts; for instance, while all primate genomes show five isochore families (L1, L2, H1, H2, and H3), fish genomes show