

Review

Impact of gene gains, losses and duplication modes on the origin and diversification of vertebrates

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ABSTRACT

The study of the evolutionary origin of vertebrates has been linked to the study of genome duplications since Susumo Ohno suggested that the successful diversification of vertebrate innovations was facilitated by two rounds of whole-genome duplication (2R-WGD) in the stem vertebrate. Since then, studies on the functional evolution of many genes duplicated in the vertebrate lineage have provided the grounds to support experimentally this link. This article reviews cases of gene duplications derived either from the 2R-WGD or from local gene duplication events in vertebrates, analyzing their impact on the evolution of developmental innovations. We analyze how gene regulatory networks can be rewired by the activity of transposable elements after genome duplications, discuss how different mechanisms of duplication might affect the fate of duplicated genes, and how the loss of gene duplicates might influence the fate of surviving paralogs. We also discuss the evolutionary relationships between gene duplication and alternative splicing, in particular in the vertebrate lineage. Finally, we discuss the role that the 2R-WGD might have played in the evolution of vertebrate developmental gene networks, paying special attention to those related to vertebrate key features such as neural crest cells, placodes, and the complex tripartite brain. In this context, we argue that current evidences points that the 2R-WGD may not be linked to the origin of vertebrate innovations, but to their subsequent diversification in a broad variety of complex structures and functions that facilitated the successful transition from peaceful filter-feeding non-vertebrate ancestors to voracious vertebrate predators.

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1. Introduction

In the 1930s, Haldane and Muller, based on cytological observations of chromosomal duplications, already hypothesized the relevance that gene duplications may have for the origin of new genes and phenotypes [1,2]. In 1970, Susumo Ohno published his famous work *Evolution by Gene Duplication* and suggested a key

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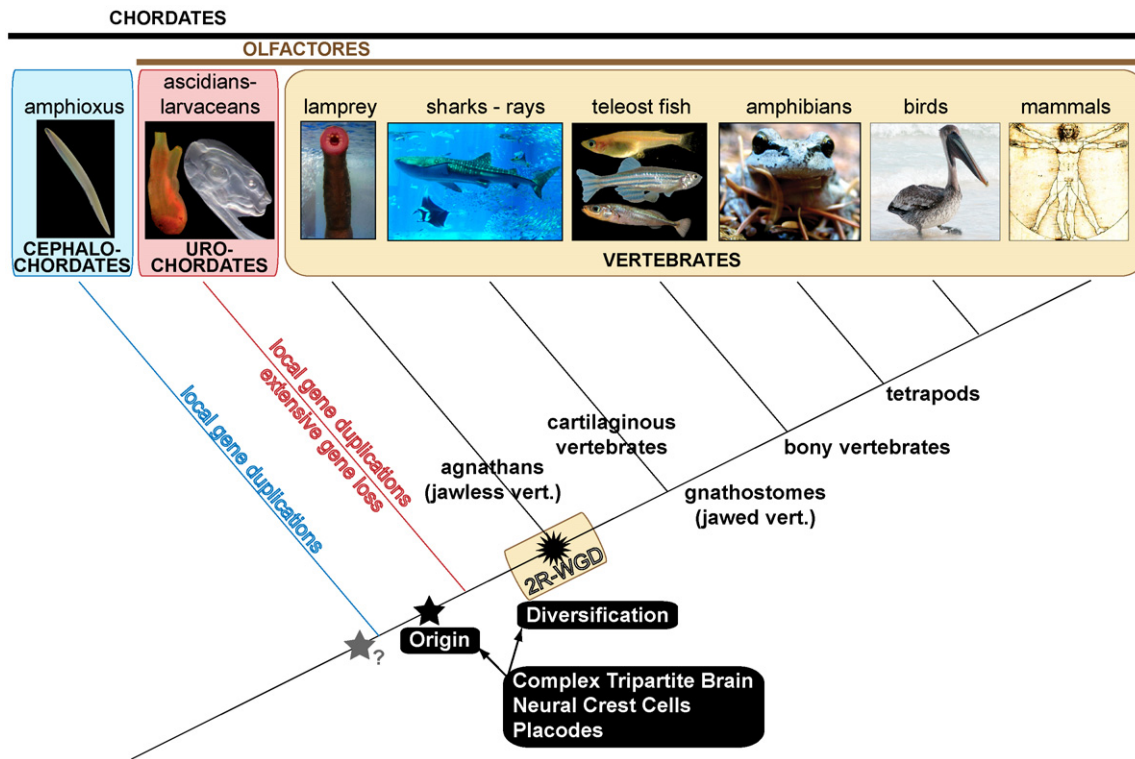


Fig. 1. Schematic evolutionary tree of chordates indicating some of the major events of genome or local gene duplication. Evidence suggests that increase of the complexity of developmental gene regulatory networks due to the 2R-WGD might have had a significant impact on the diversification (15-point black star) of vertebrate features, including structures derived from neural crest cells and placodes, as well as the development of a complex tripartite brain in the stem vertebrate. Whether the 2R-WGD was crucial for the evolutionary origin of these structures, however, remains unclear, and the hypothesis that the origin of these structures dated back to at least stem Olfactores (5-point black star) or even predated the origin of the chordates (5-point gray star) cannot be dismissed. Analysis of the gene content of the genome of amphioxus and ascidians has revealed the presence of extensive local gene duplications leading to a similar number of ancestral chordate genes duplicated in the three chordate subphyla (although the urochordates have also suffer extensive gene losses). Therefore, it is plausible to suggest that the mode of duplication (i.e. genome vs. local) might be the key event that favoring the retention of *transdev* genes, promoted the extraordinary diversification of vertebrate features.

Lamprey picture courtesy of Juan Pascual-Anaya.

role of genome duplication in the origin of vertebrates and their diversification [3,4] (reviewed in [5]). Since then, the study of the origin and evolution of vertebrates has been intimately related to the study of gene duplications.

Vertebrates belong to the chordate phylum, together with urochordates (with which they form the clade of the olfactores), and cephalochordates (Fig. 1) [6–10]. All chordates share a common basic body plan at least during the larval stage, consisting of a notochord running through a post-anal tail, a dorsal hollow nerve cord, longitudinal blocks of muscle along the notochord, and ciliated pharyngeal gill slits [11]. Vertebrates, however, develop a more complex body plan than urochordates and cephalochordates. The evolution of a complex tripartite brain and central nervous system, and convoluted structures derived from neural crest cells and placodes have been classically considered key developmental innovations that facilitated the origin and diversification of vertebrates [12–14].

Ohno's comparative analyses of genome sizes and isozyme complexity among chordate taxa led him to consider that the combination of tandem gene duplications and an octoploidization event involving two rounds of whole-genome duplication (2R-WGD) were probably key evolutionary mechanisms that facilitated the invertebrate–vertebrate transition, and the subsequent origin of vertebrates [3] (reviewed in [15]). The discovery of paralogy groups in the human and mouse genome (including the four *Hox-cluster* loci) was interpreted as remnants of these two events of tetraploidization [16–18], thereby providing one of the earliest supporting evidence of Ohno's 2R-hypothesis. The finding of a single

Hox cluster in the cephalochordate amphioxus [19], prototypical to the four clusters of mammals, suggested that the two tetraploidization events occurred after the cephalochordate–vertebrate split [20–22]. During two decades, however, doubts were casted on whether the 2R-WGD actually occurred. Alternative scenarios were proposed, implying multiple independent block duplications [23–27], or a combination of one round accompanied by segmental duplications [28–30]. It was not until recently, however, when comparative genomic mapping of different vertebrates [31] and the sequencing of the whole genome of amphioxus [10,32] provided unmistakable proof of the 2R-WGD at the origin and during early vertebrate evolution (reviewed in [33] and [34]). Despite of the definitive support gathered for the 2R-hypothesis, it should be noticed that many paralogs of the current vertebrate gene families were not originated during the 2R-WGD, but by extensive events of local duplications, which can be caused by unequal recombination, or by events of transposon mobilization or retrotransposition (reviewed in [35,36]).

Different models have been proposed to account for the maintenance and evolutionary fate of duplicated genes depending on the mechanisms (genome vs. local gene duplication) by which were generated (reviewed in [37]). Preservation of gene duplicates is favored, for instance, if the duplication affects the whole genome, as opposed to multiple individual gene duplications, because gene stoichiometry is maintained when entire gene networks are duplicated, and therefore deleterious gene dosage effects can be counteracted [38–41]. For these reasons, and to avoid confusions, the term *ohnolog*, suggested in honor of Ohno's contribution, refers

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