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Review

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The gap in research on polyploidization between plants and vertebrates: model systems and strategic challenges

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Abstract Polyploidization via whole-genome duplications (WGD) is a common phenomenon in organisms. However, investigations into this phenomenon differ greatly between plants and animals. Recent research on polyploid plants illustrates the immediate changes that follow WGDs and the mechanisms behind in both genetic and epigenetic consequences. Unfortunately, equivalent questions remain to be explored in animals. Enlightened by botanical research, the study of polyploidization in vertebrates involves the identification of model animals and the establishment of strategies. Here we review and compare the research on plants and vertebrates while considering intrageneric or intraspecific variation in genome size. Suitable research methods on recently established polyploidy systems could provide important clues for understanding what happens after WGDs in vertebrates. The approach yields insights into survival and the rarity of polyploidization in vertebrates. The species of *Carassius* and the allopolyploid system of goldfish × common carp hybridization appear to be suitable models for unraveling the evolution and adaptation of polyploid vertebrates.

Keywords Polyploidization · Recurrent WGD events · Genome size variation · Next-generation sequencing

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Polyploidization via whole-genome duplication (WGD) involves the integration of more than two complete sets of chromosomes in a cell. It occurs in many eukaryotes [1, 2]. Two mechanisms can drive it: autopolyploidization, the duplication of a species' own genome, and allopolyploidization, the doubling of chromosomes following interspecific hybridization [3, 4]. WGD may give rise to immediate genome doubling. Such duplications provide more genetic materials and yet create genomic redundancy [5]. Polyploidization occurs most commonly in angiosperms, of which at least 70 % species were thought to have experienced one or more WGD events in their history (Fig. 1) [6, 7]. In contrast, polyploidization is relatively rare in animals and it mainly occurs in some species of insects and a few vertebrates (Fig. 1) [8–10]. In this review, we discuss genetic and epigenetic events following polyploidization. We highlight challenges to investigating polyploidization, the differences between polyploidization of plants and animals, the possible explanations of why polyploidization rarely occurs in animals, and offer a

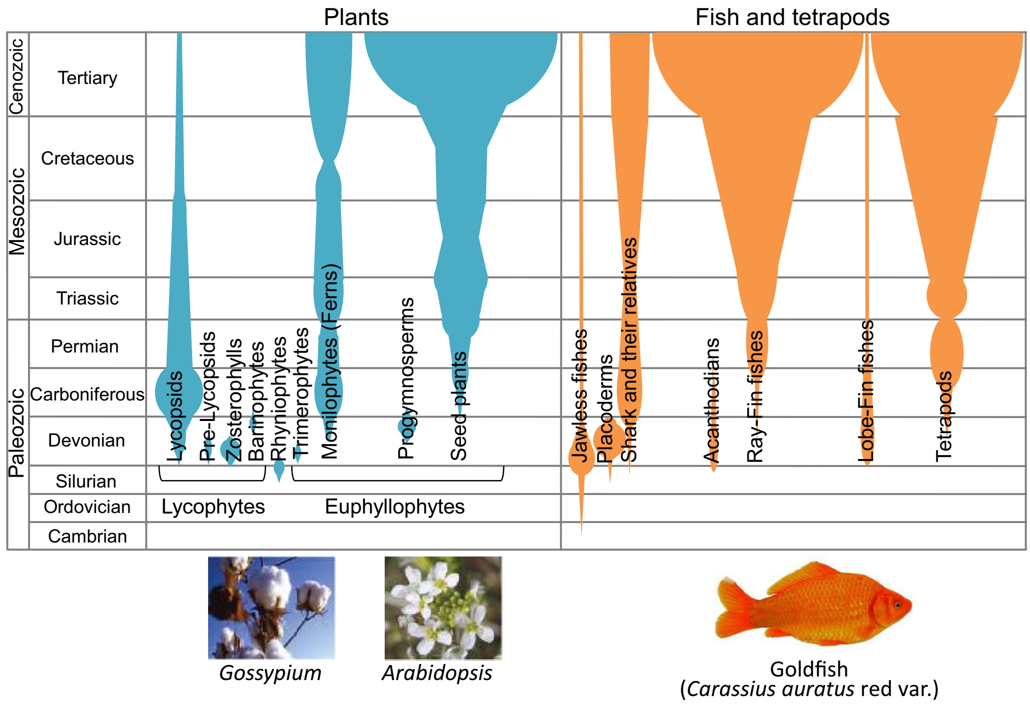

Fig. 1 Diversity of some plants, fishes and tetrapod groups according to the fossil record. The widths of colored columns indicate the relative number of species of plants and animals. The lower figures display representative angiosperms [11] and vertebrates that experienced whole-genome duplications. Adopted and modified from Murphy DC (http://www.devoniantimes.org) and Hegarty and Hiscock [11]

suitable model for investigating the phenomenon in the genomic era.

1 Intensive genetic and epigenetic changes in polyploidy lineages

Following polyploidization or WGD, redundant genetic material causes genomic shock, which can result in genomic instabilities, chromosomal imbalances and regulatory incompatibilities that ultimately result in reproductive failure. These effects include random gene loss, accelerated mutations, chromosomal rearrangements and failed paring of homologous chromosomes [12, 13]. The increased gene content might also drive changes in cell architecture and regulatory networks. These phenomena can lead to genomic chaos displayed as dosage imbalances and abnormal expressions [3]. WGD might also give rise to irregularities of mitotic and meiotic activities, which are crucial for the stability of cells and the survival of zygotes [3, 14].

1.1 Initial changes and potential drivers in newly formed polyploids

Relative to polyploids that formed a few million years ago, those originating in the last few hundreds of years might be still ongoing genomic changes [15]. Newly formed polyploids undoubtedly experience fast and large-scale changes after genome doubling [12, 16, 17]. These changes involve genetic, epigenetic and some other levels that are important for survival. The tacking of these initial changes might yield insights into the potential mechanisms and drivers of survival. This requires choosing taxa that experienced a recent WGD.

1.2 Recently formed polyploid plants illustrate great genetic and epigenetic changes

Since Hugo de Vires' initial discovery of phenotypic variants breeding true or segregated in *Oenothera lamarckiana*, which later proved to be tetraploids [18], variation in chromosome numbers and its consequences has drawn much attention. Many polyploid plants have been discovered, and today they are bred for research and their economic value.

Many naturally occurring or domesticated lineages have experienced recurrent WGD, and some involve differing levels of ploidy (Table 1). For example, wild chrysanthemum exists as diploids, allotetraploids, hexaploids and decaploids [19, 20]. Polyploid wild primrose consists of tetraploids (*Primula malacoides*, $2n = 4x = 36$), hexaploids (*P. incana*, $2n = 6x = 54$; *P. scotica*, $2n = 6x = 54$), and even octoploids and decaploids [20, 21]. In some domesticated lineages, polyploid systems were established to increase production and