Unreduced gametes: meiotic mishap or evolutionary mechanism?

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Unreduced gametes (gametes with the somatic chromosome number) are known to facilitate polyploid formation. Unreduced gametes result from a plethora of different mechanisms across different taxa, suggesting that the ability to produce unreduced gametes has evolutionary utility. Heritable genetic variation for unreduced gamete production has been observed, thereby providing an evolutionary substrate. Unreduced gametes are also frequently involved in interspecific hybridisation events as well as being produced by interspecific hybrids, facilitating allopolyploidisation. Environmental stress often triggers unreduced gamete production, suggesting that unreduced gametes may facilitate polyploid speciation in response to changing environments. Thus, although unreduced gamete formation may be a meiotic mishap, we suggest that unreduced gametes can be more explicitly considered as a mechanism for evolutionary speciation that should be measured and tested across and within lineages for exaptive evolution (a feature with evolutionary utility that has not arisen under conventional selective pressure) and evolvability (the capacity to generate adaptive genetic variation).

Polyploidy: saving variation for a rainy day

Polyploidy (Box 1; see Glossary) is prevalent across eukaryotic life, particularly in the plant, animal, and fungal lineages. It has been suggested that the rationale for this prevalence of polyploids is that it provides novel genetic and genomic variation that can allow polyploid individuals to exploit new environmental niches and outcompete their diploid progenitors [1]. Genome sequencing has revealed remnants of ancient polyploid events in the lineages of flowering plants [2], vertebrates [3], and fungi [4]. In fact, polyploidy may be a feature of most taxonomic groups: recent polyploid species have been observed in insects, crustaceans, amphibians, fishes, flatworms and molluscs [5], in mosses [6], liverworts [7], ferns and flowering plants [8], yeasts, mushrooms, and other fungi [9], and in red, green, and brown algae [10]. Mammals and birds may be the exception rather than the rule: polyploids are often formed in these animal groups but are rarely viable [11,12]. Sexually reproducing polyploids are also thought to be rare in conifers and reptiles, although the California redwood (*Sequoia sempervirens*) is a known hexaploid [13] and asexually-reproducing triploid species are common in lizards [14].

The relevance of polyploidy to speciation is itself still a topic of some contention. Despite evidence of both recent and ancient involvement of polyploidy and hybridisation in speciation, many authors still consider polyploids to be

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Glossary

Adaptation: a feature resulting from natural selection for a particular utility.

Allelic heterosis: complementation of two or more alleles (gene variants) to confer 'hybrid vigour' or a phenotypic advantage over the homozygous allelic state.

Allopolyploidy: the presence of more than one set of homologous chromosomes originating from different species within an organism.

Aneuploidy: loss or gain of additional chromosomes relative to an established karyotype or normal chromosome complement.

Asynapsis: failure of homologous chromosome pairing during meiosis.

Autopolyploidy: the presence of more than one set of homologous chromosomes originating from a single species within an organism.

Chromosome bridge: a structure resulting from a meiotic crossover event that has recombined two chromosomes such that two centromeres are present on this recombined chromosome, with subsequent formation of a 'bridge' across the metaphase plate when spindle fibres try to segregate each of the two centromeres on the same chromosome to different poles of the cell.

Chromosome laggard: a chromosome which has delayed migration to daughter nuclei during meiosis (anaphase); these chromosomes can be left behind on the metaphase plate and excluded from subsequent daughter nuclei.

Endosperm: in flowering plants, the tissue that provides nutrition for the developing embryo; usually $3n$ and generated by fertilisation of a $2n$ polar body by a sperm/pollen nucleus at the same time as the zygote fertilisation event.

Evolvability: the capacity of a system to generate heritable, adaptive diversity.

Exaptation: a feature with a utility that was not evolutionarily selected for.

First division restitution: the failure of meiosis and generally the first meiotic division to separate homologous chromosomes into daughter nuclei, resulting in two unreduced gametes.

Homoploid: involving only one ploidy level, for example hybridisation between two diploids without associated genome doubling.

Interspecific hybridisation: when two different species both contribute genetic information to form a new individual.

Transgressive segregation: observation of a phenotypic trait in progeny that falls outside the bounds of variation for that trait in the parents.

Parthenogenesis: asexual reproduction by direct development of female gametes into embryos.

Polar body: in female gametogenesis, one of the daughter cells produced after meiosis that is not fertilised to form the zygote.

Polyploidy: the presence of more than one set of homologous chromosomes within an organism.

Second division restitution: the failure of meiosis and generally the second meiotic division to separate sister chromatids into daughter nuclei, resulting in two unreduced gametes.

Unreduced gamete: a gamete with the somatic chromosome complement.

Box 1. Polyploidy and unreduced gametes

Polyploid organisms and cells are those that contain more than one set of chromosomes. In most sexually reproducing species the somatic (body) cells of an organism contain a maternal and a paternal chromosome copy, which make up one homologous chromosome pair. Homologous chromosomes generally have the same content and order of genes (e.g., eye colour), but may contain different gene variants (alleles; e.g., blue and brown). These homologous chromosome pairs match up, recombine, and then separate at meiosis to produce gametes (sex cells such as eggs and sperm in animals, and ovules and pollen in plants) with only one chromosome from each homologous pair. These gametes are referred to as 'haploid', meaning they have half the DNA content of their parent cells. The parent organism/s and cells are referred to as 'diploid', in reference to the two homologous chromosomes present in each cell. Polyploid organisms have more than one set of homologous chromosomes: either three or more copies of the same homologous chromosome (autopolyploid) or two or more sets of homologous chromosomes from different species origins (allopolyploid).

Gametes can also be polyploid. 'Unreduced' or '$2n$' gametes have the same chromosome number as the somatic (body) cells of the parent organism, in other words will be diploid in a diploid organism [38]. In humans for example, that have 23 pairs of chromosomes ($2n = 46$), an unreduced gamete will have 46 chromosomes, and a normal, reduced sperm or ovule will have 23 chromosomes ($n = 23$). 'Unreduced' then refers to the failure of the meiotic process to 'reduce' the chromosome number from the somatic to the gametic level. However, this definition is still subject to some murky interpretation. What about double-unreduced gametes, with a $4n$ chromosome complement? Can aneuploid gametes with a chromosome number intermediate between that of the $2n$ and n chromosome number still be considered unreduced? This is far from a straightforward question, particularly in the case of hybrid plants with already aneuploid chromosome numbers, or in species or genera with a non-standard form of gamete production. Unreduced gamete formation is essentially 'fixed' in many asexually reproducing species, whereby unreduced eggs subsequently develop into embryos [36,67]. However, for the purposes of this review we will refer to unreduced gametes as any gamete formed with a higher chromosome complement than can be achieved by normal homologous chromosome pairing and segregation in a sexually reproducing species.

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evolutionary 'dead-ends' [15], with extant polyploid lineages resulting from a few, rarely successful events [16]. However, the evidence for polyploid speciation events continues to accumulate [17,18]. For example, several species have been determined to result from allopolyploidy events within the past 200 years, often as a result of human activity: this has been confirmed conclusively in the angiosperm genera *Tragopogon* [19], *Mimulus* [20], and *Cardamine* [21]. Polyploidy confers definite benefits, such as the potential for neo- and subfunctionalisation of duplicate gene copies, resulting in novel genetic variation [22] and the masking of deleterious recessive alleles [18]. Allopolyploidy can confer additional advantages: novel genetic variation and phenotypes different to the parent species can be produced through transgressive segregation [18,23–25] and allelic heterosis [26]. Of course, allo- and autopolyploidy exist on a spectrum related to parental genome divergence, and 'autopolyploids' may often form from hybridisation between genetically distinct members of the same species and hence show similar behaviour to more conventional allopolyploids [27]. Hybrids formed without polyploidy (homoploid hybrids, with a haploid chromosome complement from each parent) are common [28], and may even result in new species [29,30]. However, allopolyploidisation, whereby a complete set of homologous chromosomes (diploid complement) is transferred from each species parent, tends to result in greater fertility and higher reproductive isolation from the diploid progenitors than does homoploid hybridisation [31]. Polyploidy may also mitigate genome upheaval occurring as a result of hybridisation-associated genome shock [32], and thus polyploidy may even be thought of as a mechanism facilitating hybridisation [33]. Polyploidy and hybridisation unarguably result in a wide range of novel phenotypic traits that may aid in adaptation to changing environments [18,24,25]. Together, a great deal of experimental and observational evidence and strong theoretical models support the idea that polyploidy, and particularly allopolyploidy, can be a mechanism for speciation.

Polyploidy itself is facilitated by an almost ubiquitous, oft-overlooked process: unreduced gamete formation

(Box 1). Unreduced gametes were proposed to comprise the primary mechanism of polyploid formation nearly 40 years ago: in 1975 Harlan and DeWet [34] made an excellent case for meiotic over mitotic mechanisms for polyploid speciation events. Although unreduced gametes are not the only mechanism for polyploid formation (Figure 1), substantial evidence suggests that meiotic, rather than mitotic, mechanisms are implicated in most natural polyploid formation events [12,34–37]. Previous reviews have focused on mechanisms of unreduced gamete formation [38], their ecological significance and occurrence [35], and, recently, what we now know about the molecular and cytological mechanisms underlying unreduced gamete formation [39,40]. Now, as genome sequencing becomes increasingly accessible and tells us more about the prevalence of hybridisation and polyploidy and their roles in the origins of species, the time is ripe to synthesise observations on unreduced gamete formation that occur across the
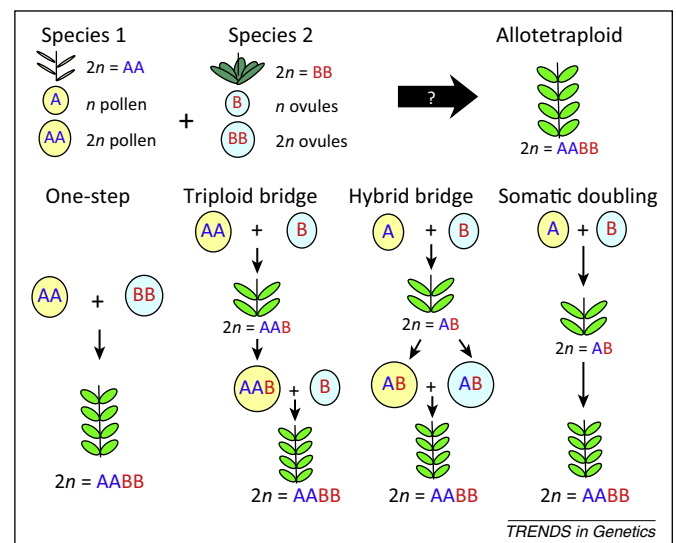
Figure 1. Possible pathways for allopolyploid formation in plants. Of the four pathways shown, the one-step, triploid bridge, and hybrid bridge pathways involve unreduced gamete formation with the formation of $2n$ pollen and/or $2n$ ovules, while the somatic doubling pathway does not involve unreduced gamete formation.