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ON Ö. WINGE AND A PRAYER: THE ORIGINS OF POLYPLOIDY[1]

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INTRODUCTION

Polyploidy is recognized as the most conspicuous feature of chromosomal evolution in the higher plants (Stebbins, 1970). Since the beginning of the century, we have learned a great deal about the taxonomic and geographic distribution of polyploids. Relationships of polyploidy to ecological adaptation, modes of reproduction, life cycles, hybridization, introgression, genetic segregation and other genetic and evolutionary features have been studied in detail. On the mode of origin of polyploids, however, we find the literature strangely equivocal. Individual observations are published and occasional reviews of the evidence presented, but many students of plant evolution either avoid the question altogether or fall back on the cliché: "hybridization followed by chromosome doubling". Indeed, "hybridization followed by chromosome doubling" has become more than a cliché; it is a veritable incantation whose magic is calculated to be strong enough to split chromosomes by constant repetition. In this paper we shall show that the cliché is imprecise at best and decidedly misleading at worst and that the modes of origin of polyploids have evolutionary significance.

In the early decades of the 20th century, when the phenomenon of polyploidy was less familiar, plant scientists showed great interest in the mechanisms by which chromosome sets were added to form polyploid series. The techniques and equipment were rather unsatisfactory at the time and some theories were put forward based more on speculation than observation. One

[1]We thought the title rather clever, but our students soon made it clear that most of the people who read genetic literature today were born after World War II and have no recollection of a wartime song, "Coming in on a Wing and a Prayer."

of the most influential was that proposed by Ö. Winge (1917). It was his impression that chromosomes from each gamete paired in the zygote and that if the gametes were so unlike that chromosomes could not pair, the zygote would perish. It might happen, however, that the chromosomes in such a zygote might split longitudinally, each making a pair, and permitting the development of a hybrid individual with double the parental number of chromosomes.

The spontaneous appearance of tetraploids in *Oenothera lamarckiana* Ser. (Gates, 1909; 1924) and the amphidiploid hybrid between *Nicotiana glutinosa* L. and *N. tabacum* L. (Clausen and Goodspeed, 1925) were brought forward as proofs of the Winge hypothesis. An alternative and much more likely mechanism was proposed by Stomps (1912) for *Oenothera*, and the *Nicotiana* example was by no means proof of Winge's theory. Indeed, no critical supporting evidence has ever come forth and a great deal has been published that clearly contradicts the concept. Nevertheless, the idea that chromosomes just "double" of their own accord has been imprinted on generations of botanists.

In 1926, Kihara and Ono published their classic paper in which they coined the terms "autopolyploidy" and "allopolyploidy". The concepts were useful at the time and still have limited value although there are so many degrees and grades between extremes that Stebbins (1970) is inclined to discontinue use of the terms. The wording of the definitions was unfortunate, however, and served to reinforce the "hybridization followed by chromosome doubling" mystique. To save the reader the trouble of digging out the old paper, we reproduce the statement:

> Unter *Polyploidie* mussen wir heute zwei verschiedene Erscheinungen unterscheiden, nämlich die *Autopolyploidie* und die *Allopolyploidie*. Unter Autopolyploidie versteht man die Verdoppelung desselben Chromosomensätzes; unter Allopolyploidie die durch das Zusammenkommen verschiedener Chromosamensätze auf dem Wege der Bastardierung erfolgte Chromosomenvermehrung.

By 1927, Karpechenko felt compelled to write: "—the origin of polyploid forms, even of those which have appeared under experimental conditions, remains in most of the cases unexplained. We are not only compelled to confine ourselves to more or less probable conjectures as to the origin of the tetraploid *Oenothera*, *Primula*, *Solanum*, *Datura*, but even in those cases where the polyploids were obtained as a direct result of hybridization, when it would seem easier to follow them, *in statu nascendi*, the process of the multiplication of chromosomes remains obscure" (Karpechenko, 1927, p. 349).

He then went on to show that in his own case of *Raphanus* x *Brassica*, it was clear that meiotic failures took place and unreduced gametes were produced. His hexaploid plants clearly did not arise from triploid zygotes by a doubling of their chromosomes but "from a fusion of tetraploid gametes with diploid ones". Buxton and Darlington (1931) concluded from their study