Polyploids and Polyploidy.¹

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ANOTHER means of variation, closed to the ordinary diploid, is open to the polyploid. This is variation by loss. Gametes of a diploid which are not equipped with the full chromosome complement are not as a rule functional, but in a tetraploid, where every part of the hereditary material is represented twice in the gametes, loss of a chromosome or part of a chromosome does not necessarily lead to non-viability and is a possible source of a new chromosome balance, a new genetic type. This kind of change is probably responsible for a great deal of the variation in that highly variable species *Tradescantia virginiana*.

It is not surprising, therefore, that many polyploid species, both in breeding behaviour and in chromosome behaviour, resemble this second type, the type of *Primula kewensis*. The hexaploid *Prunus domestica*, having three times the chromosome number of its diploid relatives, itself usually behaves like a diploid, but when it is crossed with one of these diploid relatives the hybrid behaves like a tetraploid of the *Datura* type. Pairing takes

identical chromosomes, presumably of specifically distinct origin. We must therefore distinguish between the *primary segregation* that results from the normal pairing in a polyploid, and the *secondary segregation* of the characters of its ultimate diploid parents, which results from the exceptional pairing of their unlike chromosomes. The behaviour in these cases is an exact parallel of that in the experimentally produced *Primula kewensis*.

When two hybrid tetraploid species such as *Triticum polonicum* and *T. durum* are crossed, complicated results are naturally to be expected from the combination of these two types of segregation. As in the *Prunus* hybrid, not two species but four are really concerned, and *a priori* we can have no reason for predicting one kind of pairing and segregation rather than another. Breeding results show that, in respect of certain chromosomes at least, there is regular pairing of the chromosomes derived from the ultimate diploid parents of each species, with the consequent segregation of their characters, and the suppression of the characters of the immediate tetraploid parents, which are never recovered in subsequent generations.

A hybrid in *Rubus* shows another complexity in segregation. Three seedlings were raised from a cross between the diploid *R. rusticanus inermis* and the tetraploid *R. thyrsiger*. Two of these were indistinguishable and, as might have been expected, closely resembled the tetraploid parent; they were triploid. The third, although obviously a hybrid, resembled the diploid parent more closely in seven well-marked characters which chiefly distinguished the two parental species. This seedling was tetraploid, and evidently the result of the union of a normal reduced male with a diploid female gamete. Thus where the female parent had made a double contribution of hereditary material, its genetical influence was increased.

This tetraploid seedling was fertile; the triploids were, as usual, sterile. In its breeding it showed two types of segregation: first a random segregation with the recovery of approximately 1 in 36 of the quadruplex recessive; secondly, the complete suppression of the characters of one parent. These results would be expected if the several chromosome types of the two species had varied independently, so that in one type there was indifferent affinity, in another a rigidly determined system of pairing. The behaviour of this cross, in both the first and second generation, affords a neat example of the application of the chromosome theory to the theory of interspecific hybridisation.

It may be worth while pointing out that, in so far as there are species in *Rubus*, this fertile seedling is a new species. Similarly, in so far as there are species in *Primula*, *P. kewensis* is a new species, and, in so far as there are species or genera in the *Cruciferae*, the *Raphanus-Brassica* tetraploid is a new species or a new genus. Polyploidy is therefore evidently a means of species-formation. Its

FIG. 5.—Metaphase of the second division in a pollen mother-cell of a tetraploid cherry. As a result of the formation of quadrivalents at the first division, two unequal bodies of chromosomes (13 and 19) have separated.

place not merely between corresponding chromosomes of the diploid and hexaploid, but also between corresponding chromosomes, derived each from the hexaploid, but not normally pairing. In spite of the regularity of chromosome behaviour, this analytic method of investigation is unsatisfactory from the genetical point of view, for the sets of chromosomes of the original diploid parents have probably ceased to be competent by themselves. The processes of variation found in diploids have continued in the polyploid without the same physiological restrictions. The result of splitting up the complement of a polyploid species is therefore sterility.

Hexaploid wheat or oats, when self-fertilised, breeds true in the main, but from time to time seedlings appear having the characters of related species, which have evidently remained submerged so long as the hybrid has behaved like an ordinary diploid. This segregation has been shown to follow the exceptional pairing of homologous but non-

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importance in evolution is more doubtful. Polyploids in their origin pass through a process that is virtually irreversible, and the advantages of their peculiar properties are therefore to a great extent meretricious. But if polyploids are not themselves of evolutionary importance the occurrence of polyploidy is probably a symptom of evolutionary processes, such as hybridisation, that are of great importance. Moreover, polyploids afford a field for the study of the hereditary material under conditions which apply critical tests of its properties. These must now be considered.

Since not merely the fertility of a polyploid but also the genetical behaviour in every other way depends on the pairing of its chromosomes, the conditions of this pairing are well worth our study. These conditions are evidently not simple, for chromosomes may regularly pair in certain circumstances (as in the diploid *Primula kewensis*), but rarely pair when identical mates are available. This problem we may shelve by saying that pairing depends on 'relative affinity'. But we may also get, as in triploid *Hyacinthus* and tetraploid *Datura*, the failure of association of chromosomes known to be identical or nearly so.

This problem, evidently related to the other, is not so easily dismissed. To understand it we must examine the processes leading up to 'metaphase' of the reduction division at which pairing is chiefly studied. At an early (prophase) stage in *Hyacinthus*, three or four threads, according to the number of corresponding chromosomes of a particular type, are seen to pair; that is to say, each part of each thread takes as partner a corresponding part of one of the other threads, and, furthermore, in doing so it acts independently of sections higher up and lower down the thread (see Fig. 6). We find, with three threads, one of the three is always unpaired, but it is a different one of the three that is unpaired at different points. With four threads interchanges of partner occur amongst them. Thus pairing depends not on any general affinity of the chromosomes for one another, but on the capacity of the individual parts of the chromosomes to pair. This seems equally clear from the results of genetical analysis of the forms of *Drosophila*, in which parts of chromosomes have been reversed. The basis of the affinity of chromosomes seems then to be similar arrangement of their parts. A dissimilar arrangement giving a lower affinity need not necessarily be correlated with genetic differentiation, but it nearly always will be, as it will indicate different descent.

Let us now see why these chromosomes, which probably always pair at prophase, fail to associate at metaphase. In the triploid hyacinths the failure to form a trivalent falls almost exclusively on chromosomes of a short type, and similarly with quadrivalents in the tetraploid. If the pairs formed by this type of chromosome are compared with those of the longer types, it is seen that they are relatively simple. Both kinds consist of four 'chromatids' or halves of longitudinally split chromosomes associated in pairs, but in the longer chromosomes these chromatids change partners,

forming what are called 'chiasmata,' two, three, four, or five times. In the short chromosomes, on the other hand, there is rarely more than one chiasma.

The chiasmata are formed at random both as regards number and position, and with an average frequency proportional to the length of the chromosome. Only by the failure of a proportion of chromosomes to form any chiasmata at all can this

FIG. 6.—Conjugation of chromosomes in a triploid tulip. (a) Chromosomes lying parallel in threes before association. (b) Chromosomes associated in pairs with exchange of partners.

normal frequency be maintained in the short type, for one of the three chromosomes must be associated with the other two and have two chiasmata.

The expected proportion of failure agrees approximately with the proportion (about one-fifth) of unpaired short chromosomes found. It therefore seems probable that pairing fails merely because no chiasma is established. This implies that the relationships of the chromatids at reduction are the same as at ordinary mitosis; they are attracted in pairs. The association of the chromosomes is then the result of a failure of the pairs of chromosomes that conjugated at prophase to separate, in respect of their constituent chromatids, as they came together.

If this is generally true, then short chromosomes

newly arisen by fragmentation should fail to pair regularly, and this is so wherever it has been studied, as in *Secale*, *Zea*, and *Tradescantia*. Such variation in pairing is analogous to that found in hybrids and polyploids, for in all these types the length of the chromosome pairing at prophase is reduced as compared with that in the non-hybrid diploid. It may be reduced so that in a proportion of cases chiasma-formation, and therefore pairing, fails altogether. From the opposite point of view we may say that the mechanism of reduction is fitted to give a regular segregation of chromosomes of the normal types in a non-hybrid diploid.

It would be possible for dissimilar chromosomes to pair along a sufficient length to establish a single chiasma, in the absence of competition, but with competition in a polyploid, clearly a chiasma will be most likely to be formed between the pair which is capable of association through the greater length. Differential affinity can therefore be regarded as a measure of linear identity. In this way the behaviour of the chromosomes, derived from different

species, which rarely pair in tetraploid *Primula kewensis* or hexaploid *Prunus domestica*, yet always pair in the diploid *Primula* or the tetraploid *Prunus* hybrid, is intelligible in more or less physical terms.

We have emphasised what may be called the mechanical conditions which determine the origin and variation of polyploids. This is because the physiological conditions are already widely recognised, and are not specific to polyploids, but in the study of polyploids the two types of restriction on the origin of new forms are equally evident, and it is impossible to show that one is more important than the other. Each has a final effect, and nowhere yet has any clear relation been shown between them.

This sketch of certain features of their behaviour should show that the investigation of polyploids is of importance, not merely in determining their own peculiar properties of inheritance and variation, but also in making out principles of behaviour that are equally important in the diploid organism.

Giant Aeroplanes and their Design.

THE giant aeroplane has always influenced the mind of the engineer as well as of the layman in a manner altogether out of any proportion to its practicability. Like all other structures, animal or mechanical, it is subject to the inexorable law of Nature known to engineers as the 'law of the cube'. For an established design of aeroplane with materials of unchanged quality, the law of the cube is not seriously disputed. If the proportion of useful load is plotted against surface and engine power, a well-defined family of closed isobars is obtained shrinking to a conjugate point of maximum useful load. For a braced biplane of wood with a factor of safety of 4 to 5, five tons total was a reasonable limit in pre-War days. An accumulation of detail improvements has put up this figure to seven or eight tons total weight, the disposable weight, including fuel, being about two-fifths of the total weight, and the paying load for five or six hours' flight being roughly one-fifth.

If instead of considering the useful load by itself it is considered as a fraction of the total weight, a very different conclusion is reached. The smaller the aeroplane the greater is the proportion of useful load until the indispensable weights—pilot, instruments, etc.—become a serious proportion of the total weight. A competent judge with wide experience has given the opinion that the best size from the point of view of useful ton-miles is less than two tons total weight.

The weak point in the argument is that the estimation of structural weight and aerodynamical quality is necessarily based on the best current practice, and though it is unlikely that all the competing designers in the world have missed any serious point in the theory or practice of structural design, still the possibility remains and is the standby of those who advocate the possibility and indeed the superiority of giant aeroplanes.

The history of these efforts is not encouraging.

It is not necessary to refer to the positive disasters which marked the first flight of most of the early giants. Taking only recent designs, although a number of ten to fifteen ton aeroplanes and flying boats have flown and landed without accident, and have proved at least controllable in the air, yet there has not been put forward the slightest evidence that the performance as measured by useful ton-miles has increased, and much evidence that the relative performance, useful ton-miles per ton of total weight, has fallen off badly, in the very way predicted by the law of the cube.

The latest effort to break away from the natural limitation of size is that of the well-known German designer, Dornier. In a recent paper to the Royal Aeronautical Society, he announced the construction of a giant flying boat with twelve engines, distributed along the span, in pairs, with a total power of about 5000 kw. and a total flying weight of about 50 tons. It is now announced that this real giant among flying machines has successfully arisen from and alighted on the surface of Lake Constance.

The distribution of weights along the wing is an old device for reducing the stresses on the wings in steady flight. As in all other cases of design where a compromise has to be made between conflicting requirements, this is offset by a corresponding disadvantage that the stresses in a landing, especially in an unequal landing, are increased. The wing structure is thus exposed to reversed stresses of a severe and indeterminate kind. Other serious disadvantages follow.

The device has failed in previous attempts. It is advisable to wait for authenticated test evidence before accepting the truly revolutionary forecasts made by the designer, of which the most astonishing is the increase of useful ton-miles with size without limit, not merely absolutely but in proportion to total weight.