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SPONTANEOUS CHROMOSOME ALTERATIONS IN *CREPIS TECTORUM* L.

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During the summer of 1930 many progenies derived from *Crepis tectorum* plants possessing aberrant chromosome sets were grown for the purpose of studying the transmission of chromosomal abnormalities. It was found in the great majority of cases, in full accord with expectation, that chromosomal abnormalities were transmitted as such to a certain part of the offspring. Thus, for instance, simple trisomies threw identical trisomies in proportions which varied according to the kind of the extra chromosome and according to the individual. Individuals possessing a typical chromosome structure (for instance, translocated chromosomes) transmitted their abnormal chromosomes to a certain percentage of their offspring. In three cases, however, the behavior of the tested individuals was entirely different. They produced, indeed, among their progeny not only the expected chromosomal abnormalities, i.e., aberrations identical with those which were characteristic of them, but there appeared also in the immediate offspring some entirely new chromosomal alterations, and, furthermore, these occurred in unusually high numbers. In the following pages will be given a short discussion of these peculiar cases observed among progenies 30.503, 30.511, and 30.515.

Progeny 30.503 was grown from open pollinated seed collected from a simple trisomic. It consisted of seven plants from which two were selected for cytological investigation because of their somewhat abnormal appearance. One of the two plants died early in development; the other was subjected to cytological investigation.

From the seventeen root-tips investigated thirteen proved to be entirely normal. Four of them uniformly contained an abnormal chromosome complement shown in figure 1, *d*. From an inspection of this figure one can see that the alteration involves two chromosomes, namely, the two A-chromosomes (see, for a normal complement of

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Crepis tectorum, fig. 1, *h*) which at first sight seem to be entirely lacking. Closer examination and comparison with the normal complement make it possible to give to this phenomenon an adequate interpretation. It is easy to see that two conspicuous structures have replaced the two A-chromosomes in this figure and that the large V-shaped chromosome and the other very short one are simply products of rearrangement of the material which normally composes the two A-chromosomes. Obviously, the proximal fragment of one of the A-chromosomes became detached as a diminished autonomous chromosome; the rest of the same A-chromosome (its distal fragment) has fused with the proximal end of the other, otherwise unaltered A-chromosome, making its smaller arm correspondingly longer and thus producing a large V-shaped structure.

The upper parts of the plant in question not having been investigated, nothing can be said about their chromosomal constitution. It appears probable, however, that certain shoots possessed some chromosomal abnormalities since they displayed a very low fertility. The latter circumstance would be expected in case the above described chromosomal alteration was present also in spore mother cells.

Progeny 30.511 was derived from open pollinated seed produced by a simple trisomic. From the total of forty plants, five appeared to be more or less abnormal and the remaining thirty-five were discarded. Cytological investigation of the root-tips of these morphologically aberrant individuals showed that two of them were simple trisomies of the triple-B type (like the parental plant), two were apparently normal, and one was a chromosomal chimera. Among many root-tips there was only one cytologically abnormal; it was uniformly altered in all its cells in a most conspicuous way. The alteration in this case involved the two D-chromosomes (fig. 1, *a*, *b*, and *c*). As may be easily deduced, the proximal fragment of one of the D-chromosomes became an autonomous small satellited chromosome, the distal portion of the same chromosome being permanently attached to the satellite of the second (otherwise unaltered) D-chromosome. The resulting alteration of the chromosome complement was thus expressed by the presence of one minute satellited chromosome and another very large one distinguished by its unusually large cylindrical satellite.

This particular plant did not show any abnormalities as to its fertility, etc., so that it seemed rather probable that this alteration was localized in a small part of the root system.

Progeny 30.515 came from open pollinated seed yielded by a chromosomally aberrant plant which possessed a very small spherical fragment in addition to its otherwise apparently normal chromosome complement. Among the total of twenty-four plants, five were selected for cytological investigation since they were distinguished by various morphological peculiarities. Only one of them (plant 3) was probably normal in its chromosome complement, but owing to the lack of good roots, this could not be established with full certainty. The remaining four plants were all chromosomally abnormal, and moreover, each of them in a different way.

Fig. 1. Somatic chromosomes from the root-tips of altered individuals of *Crepis tectorum*.

a, b, c, three metaphases from the single altered root of the plant 30.511-2. One of the two D-chromosomes was fragmented; its proximal fragment constitutes a small satellited chromosome, the distal portion being permanently fused with the satellite of the other, otherwise unaltered D-chromosome.

d, plant 30.503-2. One of the two A-chromosomes fragmented; its proximal fragment functions as a small autonomous chromosome; the distal portion is attached to the proximal end of the other A-chromosome thus forming a large V-shaped structure.

e, f, g, different plants from progeny 30.515 showing various chromosomal alterations.

h, a normal chromosomal complement from the chimeral root belonging to plant 30.515-2 (cf. fig. 1, g).

i, diagram showing the distribution of altered and normal mitoses in the root of plant 30.515-2 (cf. fig. 1, g). Crosses indicate altered cells, discelets, normal cells.

See also the text. Magnification 1700 diameters, except diagram i which is drawn to a much smaller scale.

Plant 1 was a simple triplo-A trisomic, all its roots uniformly possessing an extra A-chromosome.

In plant 2 one root out of fourteen was partly altered in its chromosomes. There appeared a sector forming about 75 per cent of the whole root in which the proximal fragment of one of the two D-chromosomes became autonomous (as in the case of progeny 30.503), the distal portion of the same chromosome being fused with the proximal end of one of the B-chromosomes, thus forming again a large V-shaped structure (fig. 1, *g* and *i*).

Plant 4 (fig. 1, *e*) was uniformly altered in all its roots. In this case there was present one C-chromosome extra, and, in addition, a large V-shaped structure apparently derived from fusion, as in the instances described above.

Finally, plant 5 displayed the same peculiarity as the parental individual, namely, one of its roots contained in all its cells a very small spherical fragment (fig. 1, *f*).

None of the above chromosomal abnormalities seemed to influence the mitotic process, nor did they seem to affect in the slightest degree the cell sizes or the vitality of the cells, etc. The latter was especially clear in the case of plant 30.515-2 where the sector of the root containing the altered chromosomes did not differ in regard to its cell divisions, cell size, shape, etc., from the chromosomally normal part of the root (cf. fig. 1, *i*). It should be concluded, therefore, that even such profound rearrangements of the chromosome material as those described above have no physiological effect whatever, at least so far as roots are concerned. One can hardly doubt, moreover, that they also produce no effect upon any other somatic tissue, at least in the earlier stages of its development.

The observations reported here not only add some new cases of chromosomal alterations to those previously known to occur in *Crepis* spontaneously (M. Navashin, 1926) or after the x-ray treatment (M. Navashin, 1931), but they also throw some light upon the conditions under which such chromosomal alterations are most likely to occur. First, it may easily be seen that in the majority of cases they originate in somatic mitoses and sometimes very late in ontogeny because the majority of individuals developing them are chimeras. Secondly, it seems probable that there exists some peculiar condition in certain individuals, which makes their chromosome structure and the chromosomal distribution labile and subject to frequent alterations in various ways. It may be suggested that just these three individuals which

gave rise to the progenies reported above possessed some inherent and perhaps heritable instability of chromosome behavior, which could account for the fact that, of their offspring, an unusually high proportion of individuals was altered in several different ways. It is necessary to point out in this connection that the frequency of spontaneous chromosomal alterations normally does not reach even 0.1 per cent, while in the above cases the corresponding frequency was almost one hundred times as high.

While chromosomal alterations representing only rearrangements of the chromosome material (dislocations) could hardly produce any immediate visible effect, some of them would inevitably lead to changes in chromosome affinity. Thus, for example, if plant 30.515-2 (fig. 1, *g*) could transmit its chromosomal peculiarity in homozygous form, individuals could arise which would possess an entirely new mode of chromosome conjugation in meiosis. From what is known now of homozygous translocation in *Drosophila melanogaster* (Dobzhansky, 1930), such organisms can really exist and, moreover, can be fertile. If, now, such an individual should be crossed with the original normal form, the hybrid would inevitably suffer from meiotic disturbances involving the translocated chromosomes, in the case referred to above, chromosomes B and D. For the normal B-chromosome will be attracted by one part of the fusion chromosome, the D-chromosome will tend to conjugate with the other part of the fusion chromosome, and the small free fragment of the D-chromosome will be attracted by the corresponding part of the D-chromosome. In such a hybrid normal reduction division would be impossible and the homozygous form possessing the dislocated chromosomes would become more or less genetically isolated from its progenitor. Thus it seems probable that certain chromosome alterations of the type described above may play an important rôle in the initial steps of species formation.

It should be noted that alterations originating in undifferentiated sporophytic tissue would have a decided advantage over those arising during gametogenesis. For, in case the altered sporophytic tissue should produce reproductive organs, altered functional gametes might arise at once in great numbers and thus the new chromosome organization would be transmitted to the offspring more certainly than in the case of occasional formation of single aberrant germ cells during sporogenesis.

The above facts may be advantageously applied also to the explanation of some characteristic chromosome relations existing among

species. Thus, for instance, the origin of the large V-shaped chromosomes typical of many species, especially of the *pulchra*-group in *Crepis* (Babcock and Navashin, 1930) may be attributed with a fair degree of probability to fusion of the sort described above. The occurrence of very small satellited chromosomes (for instance, in *Crepis parviflora*, *loc. cit.*) may be explained as a result of fragmentation, since the D-chromosomes are especially apt to detach free proximal fragments. Finally, chromosomes with unusually large satellites, as in *Crepis setosa* with its unique satellited chromosome, could arise through translocation of a considerable chromatin portion to the satellite (cf. fig. 1, *a*, *b*, and *c*).

All these considerations are concerned with translocations or mere rearrangements, first designated dislocations (M. Navashin, 1926). If, in addition, some gain or loss of chromosome material takes place, one would deal with the change of genic balance, and, consequently, with more or less far-reaching changes in the organization of the individual bearing in its cells these new genetic conditions. It is obvious that any heterozygous dislocation would ultimately result in gain and loss of chromatin material in succeeding generations owing to segregation of chromosomes. And, if not incompatible with life, these may result in variations of evolutionary significance. For there can be hardly any doubt that the evolution of *Crepis* species was primarily based upon changes in the quantity of the material contained in the individual chromosomes (cf. Babcock and M. Navashin, 1930).

Further investigation is now in progress. Attention will be devoted chiefly to the study of the transmission of the presumed hereditary lability of chromosome behavior and to the problem of obtaining homozygous translocations.

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