HETEROMORPHIC A CHROMOSOMES OF THE TOMATO DIFFERING IN SATELLITE SIZE*[1]

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In cultivated tomato plants which were largely but not exclusively derived from triploids, chromosomes of two distinct sizes were found associated with the nucleolus in the pollen mother cells. Since a trivalent was found on the nucleolus in the simple trisomic type, triplo-A only, evidently it is the A or first chromosome which is dimorphic. At somatic metaphase this chromosome has a distinct satellite. Satellites of two sizes were found on the nucleolus in early prophase of somatic mitosis, and the difference in the length of the satellites corresponded to the difference in the length of the respective A chromosomes in the pollen mother cells. It is the length of the satellite which differs in long and short A chromosomes, the remainder of the chromosome appearing the same. Diploid plants have either a pair of long A chromosomes ("long long"), a pair of short ("short short"), or a long and a short A chromosome ("long short"). The remaining eleven pairs of chromosomes show no corresponding size difference or changed association in long A long A, short A short A, or long A short A plants.

OCCURRENCE AND TRANSMISSION OF THE TWO CHROMOSOME TYPES

Lycopersicum pimpinellifolium Mill., four races resembling *L. Humboldtii* Dun., from Mexico and Guatemala, F_1 hybrids between these and *L. pimpinellifolium*, and three races resembling *L. cerasiforme* Dun. from Mexico and southern California were short short. Single plants of the cultivated varieties King Humbert, Yellow Peach, and Norton were also in this category. Long A chromosomes were first observed in the F_2 progeny of a simple trisomic, triplo-H F_1 plant from a triploid hybrid × diploid. In F_2 the four diploid and three triplo-H plants examined were all long long, and in F_3 five of the progeny of one triplo-H plant were also long long. A triploid of different origin had three long A chromosomes. F_1 hybrids between short A and long A races were long short. In F_1 from a triplo-A plant with three short A chromosomes and a long long diploid, three of the diploid plants were long short, and two triplo-A plants were short

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short long. At diakinesis in the latter, pairs of chromosomes were observed which were long short or short short, either a short or a long A chromosome remaining separate.

The size of the A chromosome is a constant character and is transmitted through the gametes to the progeny. As self-fertilization is the rule in tomatoes, after a few generations, if the three chromosome types are equally viable, long short plants would be eliminated. Long A chromosomes are not peculiar to plants derived from triploids or their derivatives in our cultures. A plant from seed sent to us by Dr. J. W. MACARTHUR of the UNIVERSITY OF TORONTO was long short. F_1 hybrids between two races sent by him and our long A races were long long so that at least one long A chromosome was present in his races. Another long long came from seed collected in Peru by Dr. S. V. JUZEPCZUK, of the Botanical Garden, Leningrad.

The progeny from selfing a long short triplo-B plant consisted of 45 diploid and 42 triplo-B plants. The A chromosomes of 47 plants taken at random were studied. They consisted of 16 long long, 18 long short, and 13 short short plants. This suggests that a long short plant forms long A and short A gametes in nearly equal proportions but that the three combinations resulting may not be equally viable. The deviation from a 1:2:1 ratio is not significant, as $X^2 = 3.0$ and $P = .23$. No characteristic phenotypic difference was found between long long, long short, and short short plants in this population or in various other populations. It is possible, however, that long long, long short, and short short plants may be distinguishable in a line which is homogeneous except in satellite size.

The A (first) chromosome of the tomato has been found to contain the loci of d_1, *p*, *o*, and *s*. The triplo-B plant C297–1 was long short and was heterozygous for d_1 and for *y*, *c*, and *u*, which MACARTHUR (1934) has found to be in the third, fourth (H), and seventh chromosomes, respectively. In the whole F_2 progeny of C297-1 the ratios were approximately

TABLE 1

Dominant and recessive phenotypes in diploid and triplo-B F_2 progeny of long-A short-A Triplo-B plant C297-1 (chromosome length was determined in part of the progeny).

A CHROMOSOMES	NUMBER OF PLANTS									
	DIPLOID	TRIPLO-B	D_1	d_1	*Y*	*y*	*C*	*c*	*U*	*u*
Long long	10	6	10	6	14	2	12	4	13	3
Long short	7	11	14	4	17	1	12	6	14	4
Short short	3	10	8	5	11	2	9	4	10	3
Not determined	24	6	18	12	16	5	23	7	16	10
Total	44	33	50	27	58	10	62	21	53	20

those of disomic inheritance (table 1). In the part which was studied cytologically, no association was found between A chromosome length and the characters determined by the D_1d_1, *Yy*, *Cc*, *Uu* gene pairs or the presence of the extra B chromosome. Short A chromosomes were found in a plant containing the three alleles D_1, *P*, and *S*, and in one containing the alleles d_1, *p*, *o*, and *s*, of the A (first) chromosome. Two plants with three short A chromosomes probably had the constitution $d_1PS/D_1pS/D_1Ps$. There is no doubt, therefore, that the d_1, *p*, *o*, and *s* loci are present in the short A chromosome.

No association was observed between the length of the A chromosomes and vigor, pollen production, or fruitfulness, except in one case which is rather suggestive. In one long long F_2 population of 123 plants, 8 diploids had almost no fruit and 4 others were intermediate between the unfruitful and the normal plants. In the unfruitful plants, no irregularities were observed in mid-prophase or later in the pollen mother cells; the pollen was normal in appearance, and these plants were otherwise indistinguishable from their diploid sibs. The F_3 progenies of two fruitful diploid and of one triplo-H parent were all normal, but the F_3 diploids from the other triplo-H parent consisted of 36 fruitful, 18 unfruitful, and 7 intermediate. In these populations inheritance of *r* and *y* was disomic, and of *c*, trisomic.

CYTOLOGICAL TECHNIQUE

Smears of pollen mother cells were fixed in Nawaschin's solution and stained in gentian violet, according to a method suggested to us by Dr. S. H. EMERSON, of the CALIFORNIA INSTITUTE OF TECHNOLOGY. In a few cases safranin or acid fuchsin was used to differentiate nucleolus and chromatin. Somatic mitosis was studied in sections of root tips 8 microns thick, using the same fixatives or the 2B fixative (LA COUR 1931) and gentian violet.

SIZE OF TOMATO CHROMOSOMES

With the exception of the long A, the chromosomes of the tomato are rather similar to one another in size both in meiosis and mitosis (plate 1, figures A-F). A study of diakinesis in pollen mother cells of some of the trisomic types has shown that the H chromosome is one of the two smallest, whereas the short A, and the B, I, and J chromosomes are relatively large. The long A chromosome is decidedly longer than any other at diakinesis. We did not find that the chromosomes of *Lycopersicum pimpinellifolium* are smaller than those of *L. esculentum* at first metaphase in pollen mother cells (plate 1, figures E and F), as described by LINDSTROM and HUMPHREY (1933). AFIFY (1933) pictures the reverse condition; chromosome size differs to this extent at metaphase in different cells

of the same smear. The four much smaller pairs figured for the tomato by COOPER (1931) have never been observed.

A CHROMOSOMES IN MEIOSIS AND SOMATIC MITOSIS

Before pachytene, while the other chromosomes are in a tangled skein the A pair consists either of a very deeply stained area near the nucleolus and slender paired threads, or the whole pair may be more deeply stained and somewhat in advance of the rest. At pachytene the A pair is associated with the nucleolus by means of a deeply stained body like that found on chromosome VI of corn and called by MCCLINTOCK (1934) the nucleolar-forming body. Extending from this body in one direction are two satellites which are usually, but not always, unpaired, broader, and more densely stained than the rest of the chromosome (plate 2, figures A-I). In the other direction from the nucleolus-forming body, which may be divided at an early stage, lies the main portion of the chromosome pair, which ends in a paler whip-like region. Separation of the pairs begins at the nucleolus-forming body and proceeds toward this paler, achromatic end. At early diakinesis the A pair is usually crossed near this end, often also near the nucleolus-forming body. At late diakinesis the pair is connected at the non-satellited end by slender crossed strands ending in small knobs which are probably derived from the pale whip-like end seen at pachytene. These knobs look like minute satellites; they can be seen only in deeply stained pollen mother cells and disappear at metaphase. The chromosomes remain attached at this end until anaphase. The true satellites cannot be distinguished in the later stages of meiosis.

In somatic metaphase short A chromosomes are distinguished by the presence of a small satellite (AFIFY 1933). Four distinct regions can be recognized: the satellite, the achromatic thread, and an intermediate region partially constricted from the fourth or main portion of the chromosome (plate 1, fig. A). This partial constriction probably indicates the position of the spindle-fiber attachment. DARLINGTON (1932, fig. 4 III N) figures a tomato chromosome with a terminal satellite and also an intercalary satellite. He says: "This chromosome has led to difficulties in counting chromosomes in Solanum, see WINKLER, 1916." We have never observed an intercalary satellite on the A chromosome of the tomato. The small terminal satellites become separated from their chromosomes in the prophase of mitosis, remaining as two compact, densely staining bodies on the surface of the nucleolus (plate 2, figures L–M), while the remainder of the short A and all of the other chromosomes are faintly stained threads. The satellites remain in this position until the disappearance of the nucleolus at the onset of metaphase. In some cells they are slightly out of the

PLATE 1

The drawings were made with the aid of a Zeiss camera lucida. The magnification is ×3070.

SOMATIC METAPHASE OF THE TOMATO

FIGURE A.—The small satellites and the attachment constriction of the short A chromosomes.

FIGURE B.—The small satellites divided, the large dividing in long A short A.

FIGURES C and D.—Typical plates of long A long A.

DIAKINESIS

FIGURE E.—*Lycopersicum esculentum.* Only one of the short A chromosomes lies on the nucleolus.

FIGURE F.—*Lycopersicum pimpinellifolium.*

FIGURE G.—*Lycopersicum peruvianum* Mill., showing two pairs of chromosomes decidedly larger than any others, both connected by unusually distinct crossed strands. The long A pair lies on the nucleolus.

FIGURE H.—Typical short A short A chromosomes at diakinesis.

FIGURE I.—Typical long A long A chromosomes at diakinesis.

FIGURE J.—Typical long A short A chromosomes at diakinesis.

Figure K.—Lateral meiotic metaphase; typical appearance of the long A long A pair and other chromosomes.

FIGURE L.—(1) Typical long A long A at first meiotic metaphase. (2) Typical short A long A at first meiotic metaphase. (3) Typical short A short A at first meiotic metaphase.

FIGURE M.—Sister plates in meiotic anaphase. The long A chromosomes are at the extreme right in each plate.

INTERKINESIS OF MEIOSIS

FIGURE N.—The long A chromosome is associated with a small nucleolar vesicle in each sister nucleus, and one larger nucleolus is present in one, two in the other.


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b
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d
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plate at this stage so that twenty-six apparently separate bodies can be counted; in other cells they are clearly terminal satellites (plate 1, figure A). They are decidedly smaller than any chromosome. At anaphase they are small, deeply stained spheres and lag slightly behind the rest of the chromosomes (plate 2, figure T). They often appear to be surrounded by a clear area. Possibly these small satellites may account for the fragments found by HUSKINS and CRANE (1930) in some somatic cells of tomato rogues.

In the satellite of a long A chromosome, one can sometimes recognize at pachytene the point which corresponds to the end of the satellite of a short A (plate 2, figure F). The long A chromosome is identical with the short A except for the length of the satellite, which is approximately two-thirds longer than that of short A. Some smears of pollen mother cells of long long plants, but by no means all, show many cells with two nucleoli. In some cells a small, rounded, deeply stained body lies on one side of the long A pair, a typical nucleolus on the other; in others a small nucleolus (as indicated by its staining reaction) lies on one side, a larger one on the other (plate 2, figure I); in still others the two nucleoli are of about the same size. When two nucleoli are present, the A chromosomes always lie between them (plate 2, figure H). It seems probable that the precocious separation which begins at the satellites and proceeds through the nucleolus-forming body may divide it into two parts which, if separate enough, function independently. At diakinesis the nucleolus is always single in the tomato. At early diakinesis the long A chromosomes are normally paired at the attached end but usually diverge sharply from about the region of the nucleolus-forming body so that each chromosome may be L-shaped. The long long pair is easily recognized at meiotic metaphase both by its large size and by its peculiar shape (plate 1, figures K and L1) and can be distinguished at every succeeding stage. It sometimes lags slightly. The spindle-fiber attachment is near the base of the large satellite, and so is far nearer the center of the chromosome than in short A.

At interkinesis, following the first meiotic division, two or three small nucleoli are present in each daughter nucleus (plate 1, figure N). Since the chromosomes do not go into a resting condition one can often see the long A chromosome in each sister nucleus with a small nucleolar vesicle attached to one side. All nucleoli disappear at second metaphase.

In somatic prophase of long long plants two large satellites lie on the enormous nucleolus, which occupies about 1/9 the volume of the nucleus as compared with about 1/43 in the prophases of meiosis. Slender paired threads can be seen passing away from the satellites in some cases. The threads are often invisible because, except in lightly stained cells, the

PLATE 2

The drawings were made with the aid of a Zeiss camera lucida. The magnification is ×3070.

THE A CHROMOSOME OF THE TOMATO AT PACHYTENE AND DIPLOTENE

FIGURES A–C.—Two short A chromosomes.

FIGURES D–F.—One long and one short A chromosome.

FIGURES G–I.—Two long A chromosomes.

FIGURES J and K.—*Lycopersicum peruvianum* Mill.

THE SATELLITES OF THE A CHROMOSOME ON THE NUCLEOLUS IN SOMATIC PROPHASE

FIGURES L and M.—Short A short A.

FIGURES N and O.—Long A long A.

FIGURE P.—Long A short A.

THE LAGGING SATELLITES AT OR JUST PRECEDING SOMATIC METAPHASE

FIGURE Q.—The elongation of the nucleolus before metaphase and lagging long and short satellites in long A short A.

FIGURE R.—Lagging of two large satellites, one above and one below the plate, with consequent lagging of the remainder of the A chromosome.

FIGURE S.—Both large satellites are on one side of the forming metaphase plate.

SOMATIC ANAPHASE

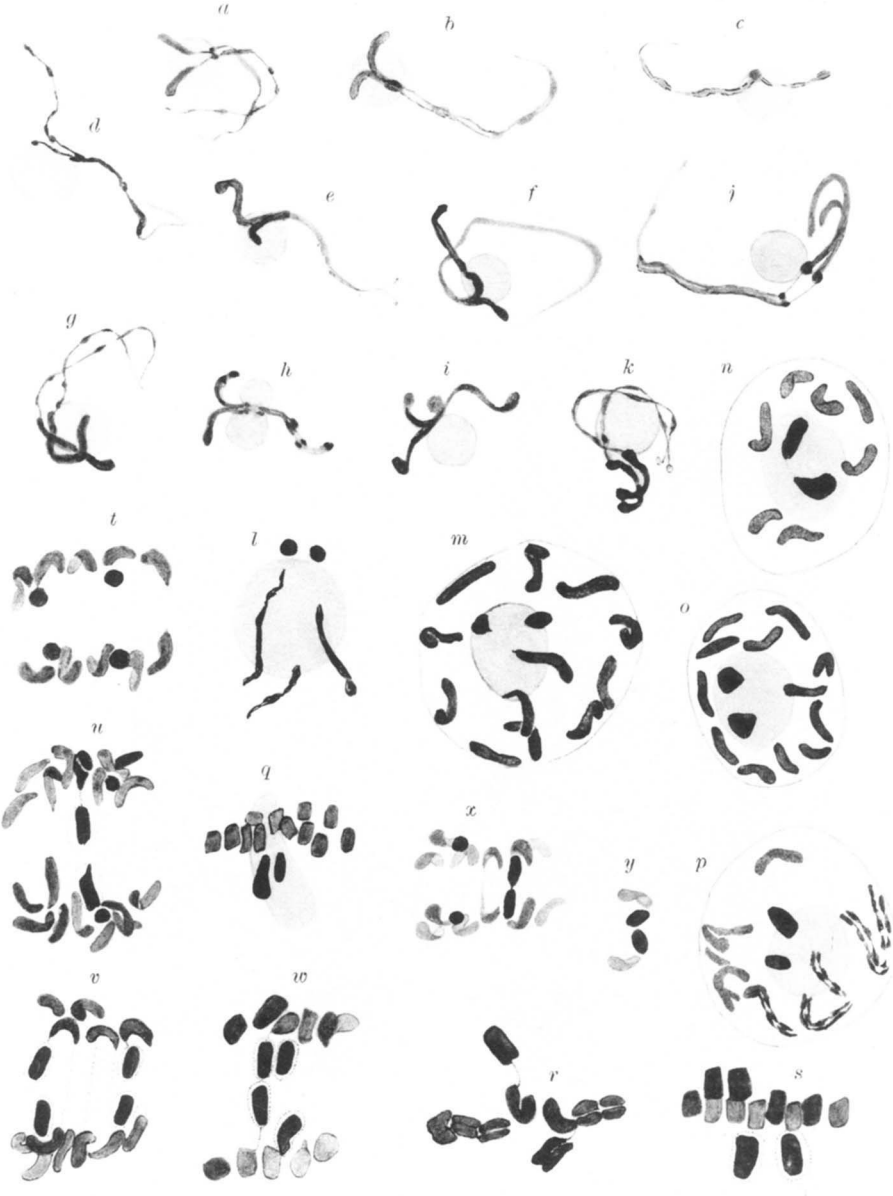
FIGURE T.—The ball-shaped small satellites passing to the poles in short A short A.

FIGURE U.—Late anaphase of long A short A with one round small satellite and one lagging large one passing to each pole.

FIGURES V and W.—Late anaphase of long A long A with two large satellites lagging in each figure. They are more commonly as in W.

FIGURE X.—Early anaphase in long A short A. The large satellite just dividing, the small satellites passing toward the poles with most of the chromosomes.

FIGURE Y.—The long A chromosome at a slightly earlier stage of division.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nucleolus is not faint enough to allow the satellites to be distinguished. These satellites are similar in length to the smaller chromosomes but are somewhat broader and darker. They lie side by side and slightly out of the plate even at metaphase (plate 1, figures C and D) and usually appear to be separate from the long A chromosomes so that the satellites might be counted as two chromosomes. At anaphase the satellites lag consistently. They often take a deeper stain than the rest of the chromosomes and appear to be surrounded by a clear area (plate 2, figures V and W).

In meiosis, the long short pair looks at all stages just as one might expect from the description of the short short and long long. Neither chromosome influences the size of the other in the sense of dominance. They pair normally from the faint slender end to the nucleolus-forming body, and the large and small satellites are usually unpaired at pachytene (plate 2, figures D–F). At first meiotic metaphase and all succeeding stages the long A and short A chromosomes are easily distinguishable (plate 1, figure L2). The members of a pair segregate regularly at the first division.

In somatic prophase a large and a small satellite are found on the nucleolus (plate 2, figure P); and immediately preceding metaphase, while the nucleolus is disappearing and thereafter, a large oblong and a small satellite can be seen slightly out of the plate (plate 2, figure Q). As in short short, the small satellites lag somewhat, but the large ones lag decidedly behind the rest of the chromosomes as in long long. The large satellite divides more slowly than the small satellite and the rest of the A chromosome (plate 2, figures X and Y).

It is not yet clear why the satellite is more distant from its chromosome in mitosis than in meiosis. The strand appears to elongate in proportion to the size of the nucleolus and may be thought of as increasing in length in proportion to the demand made upon it or as being forced away from its chromosome by the developing nucleolus. S. NAWASCHIN (1927) states that it is longer in meristematic tissue, shorter or absent at metaphase in differentiated somatic tissue and in meiosis, and longer again in pollen cells. In other words, the strand is longer in rapidly growing and dividing cells which have large nucleoli, and shorter in less active ones which have smaller nucleoli. Longitudinal sections of tomato roots show that nucleoli are progressively smaller above and below the region of rapid mitosis.

DISCUSSION

S. NAWASCHIN (1927) has described dimorphism of the nucleolar chromosomes of *Galtonia candicans* and *Muscari tenuiflorum* caused by a much slighter difference in satellite size than that in the tomato. He found only two types of plants, one with two large satellites (symmetrical races), the

other with a large and a small satellite (asymmetrical races). He believes that the form with two small satellites is non-viable, and that with two large satellites much less viable than the asymmetrical type. MEDWEDEWA (1929) studied genetically a race of *Crepis dioscoridis*, first discovered by M. NAWASCHIN (1926), that had chromosomes differing in satellite size. By selfing he obtained the ratio of 1 ++:2 +−:1 −− plants, + representing the large and − the small satellite. The ++ plants formed a marked rosette of leaves which were darker green and more deeply cut, bloomed later, and were more vigorous than −− plants; the +− plants were intermediate. The evidence indicates that in Galtonia, Crepis, and Muscari, part of a satellite is missing, and that −− plants tend to be either non-viable or less vigorous than those with a larger amount of satellite material. This is in accord with the work of BURNHAM (1932), who has shown that in maize a deficiency in a part of a satellite of chromosome VI (*Y−pl*) may reduce the viability of the eggs but does not entirely prevent them from functioning or cause abortion of the microspores. EMME (1925) found many races of Hordeum which he believed were permanently dimorphic with respect to the presence or absence of a satellite. Races were found with one or two satellites, and he concludes that plants without satellites are non-viable. In Matthiola (PHILP and HUSKINS 1931) the absence of a satellite probably acts as a pollen lethal. Apparently a certain amount of satellite material is necessary to the full development and vigor of a plant. In the tomato, a slight and non-significant deficiency of long short plants was found, but all short short plants were vigorous and fruitful and only short A chromosomes were found in all the wild races studied.

The case of the tomato shows that a considerable difference in the amount of satellite material is consistent with full vigor and fertility, and indicates that short short plants contain an adequate amount of this material. In the breeding work with the tomato, no plants have been found lacking either a whole chromosome or a chromosome fragment. The occurrence of unfruitful plants in one long long population was probably due to segregation of genes since the other long long F_2 plants and some of the F_3 progenies were entirely fruitful.

Except in Crepis, no association has been found between the phenotype and the amount of satellite material present. In the tomato, eleven of the twelve expected simple trisomic types are known and three or four types containing different chromosome fragments in addition to the normal complement. The presence even of a fragment consisting of less than half a chromosome causes a difference in the phenotype. The genetic evidence indicates that four known genes are present in the short A and that the

genes at one of these loci segregate independently of chromosome length; therefore the locus of these genes is in the region common to long and short A chromosomes. It seems probable that the extra satellite material in the long A chromosome of the tomato, as in most of the cases already cited, is genetically inert and that this condition is characteristic of satellite material. It would seem probable that a portion of a chromosome must be genetically inert before it can be either reduced in size or reduplicated without affecting a plant adversely. The Y chromosome of *Drosophila melanogaster* is characterized, as are satellites, by pycnosis and contains only one known gene (STERN 1927). The XO male fly is normal in appearance but infertile (BRIDGES 1916). The Y pairs with the X for a short distance only (METZ 1926). WILSON (1925) emphasized the fact that the Y chromosome is probably degenerating and doomed to disappear in many cases. Pycnosis and failure of complete synapsis seem to be associated, and this may be due to the absence of genes both in the Y chromosome and in satellites. Both the cytological and the genetical evidence indicate that the satellite material is different from the remainder of the A chromosome in the tomato.

Weak pairing of the terminal knobs of the satellites of maize has been observed by BURNHAM (1932) in a plant heterozygous for an interchange. The presence of chains instead of the expected rings is attributed to the fact that one of the interchanged pieces is short. It seems possible that in maize precocious shortening of the satellites interferes with pairing and prevents the formation of the expected rings. In the tomato, neither chains nor rings were found.

Evidence is accumulating to show that chromosomes with satellites, like sex chromosomes, are associated with the nucleolus at both meiosis and mitosis. HEITZ (1931b), after a careful study of the chromosomes of many species of Vicia, concludes that when a chromosome has a satellite, the nucleolus originates on the strand which connects the satellite to its chromosome. He believes that every species will be shown to possess at least one pair of chromosomes with satellites since this has been shown to be true in numerous species of the genera Crepis, Thalictrum, and Vicia. DEMOL (1928) showed that the maximum number of nucleoli in polyploid hyacinths was correlated with the number of chromosomes in the monoploid group having secondary constrictions. HEITZ (1931a) has amply confirmed this, showing further that the size and position of the nucleoli in telophase corresponds to the size and position of the satellites at anaphase. This is also true of the tomato, for in the roots of long short plants in which mitosis is proceeding rapidly, in telophase two nucleoli, one about two-thirds larger than the other, were frequently found. Cells with two

nucleoli were not seen in long long or short short root cells. It is believed that in long short plants unequal lagging of satellites leads to a difference in the time at which nucleoli are formed by the two A chromosomes. Later the two nucleoli fuse, since no cells with two nucleoli occurred in the roots of long short plants not containing division figures.

McCLINTOCK (1934) has shown that in maize a mass of chromatin which functions as a nucleolus-forming body appears on each chromosome near the satellite at pachytene. In the tomato, a similar body seems to change into a nucleolus. The position of the chromatin-rich satellite, which differs markedly in behavior and appearance from the rest of the A chromosome and is limited or lacking in gene content, suggests that the satellite may be a reservoir of material for nucleolus production. The nucleolus-forming body seems to correspond to the polar granules found on the chromosomes of Phrynotettix which WENRICH (1916) suggests are enlarged chromomeres. Each gives rise to a small nucleolus and all coalesce at the bouquet stage to form a single large nucleolus. The bouquet stage is absent in many organisms, including the tomato, and possibly it occurs only in forms in which all or several chromosomes contribute to the formation of the nucleolus. HEITZ (1931b) has shown that in Vicia nucleoli can arise from non-satellited chromosomes when those with satellites are absent.

Heteromorphy, although it has been described for autosomes, is far more frequent among nucleolar chomosomes. WILSON (1925) and SCHRADER (1928) give as cytological peculiarities of sex chromosomes heteropycnosis, lagging or early segregation, association with the nucleolus, and, in some forms, differences in size and shape. Evidently nucleolar chromosomes may possess these characteristics whether they are related to sex determination or not. According to DARLINGTON (1932), chromosomes may become differentiated as a result of fusion, fragmentation, translocation, or interchange. In the tomato, no difference in fertility, viability, or pollen development is associated with the difference in satellite size, and the extra satellite material seems to be genetically inert. It is difficult to understand how the heteromorphic condition arose, especially since, as noted above, no rings or chains of chromosomes are formed in long short plants. Satellites occur only on the A chromosomes in the tomato. Therefore, it seems probable that the added satellite material came from an A chromosome.

There is some evidence to show that the difference in the A chromosomes of the tomato may be the result of early hybridization. The tomato which was first introduced into Europe was probably unlike any known wild-type, being relatively large, ribbed, and oblate. *Lycopersicum esculentum* Mill. merely represents a group of cultivated varieties and seems to be

unknown as a really wild species. The closely related *L. pimpinellifolium* is endemic in Peru and probably in other parts of South America, but all the wild-growing races of Mexico and Guatemala are believed to have escaped from cultivation. Dr. PAUL STANDLEY, of the FIELD MUSEUM, Chicago, writes (unpublished letter) that in his opinion the tomato was introduced into Mexico before the coming of the Aztecs. The plants of *L. pimpinellifolium*, *L. Humboldtii*, and *L. cerasiforme*, which we have examined all have short A chromosomes. No probable ancestor with long A chromosomes has yet been found. It is of some interest as showing that such races may have existed, that *L. peruvianum* Mill. (*Solanum peruvianum* Jacq.), a native of Peru known as *tomate cimarrón*, seeds of which were kindly sent to us by Dr. AUGUSTO WEBERBAUER, has twelve pairs of chromosomes including a nucleolar pair with large satellites much like the long A chromosomes. One of the other pairs is also large; otherwise the chromosomes look like those of *L. esculentum* (plate 1, figure G; plate 2, figures J–K). This species is morphologically very distinct from a tomato, but its pollen applied to tomato stigmas readily causes fruit setting although the seeds are non-viable.

SUMMARY

The A (first) chromosomes of the cultivated tomato are associated with the nucleolus and are of two types, long and short, differing only in satellite size.

All wild races thus far examined have short A chromosomes. Diploid F_1 hybrids from long long × short short races have a short and a long A chromosome and in F_2 short short, long short, and long long types occur in the ratio 1:2:1. The three types are phenotypically indistinguishable, indicating that the satellites are genetically inert. The nearly related *Lycopersicum peruvianum* Mill has long A chromosomes.

The satellites are pycnotic and loosely paired at pachytene but cannot be distinguished at diakinesis. The nucleolus appears to arise on the A chromosome at the junction between the satellite and the rest of the chromosome from material which at first stains like chromatin. In prophase nuclei of meristematic cells the satellite is on or very near the nucleolus and the large satellites lie slightly out of the metaphase plate and lag at anaphase. When two nucleoli occur in long short meristematic cells, one is large, the other small, indicating a correlation between size of satellite and of nucleolus.

Both cytological and genetical evidence indicate that long and short A chromosomes are homologous. Neither shows any tendency to associate with any other chromosome.

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