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# Cytological Evidence on the Origin of Sweet Potato

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**Summary.** The results of intensive meiotic studies, particularly of the karyology and chromosomal homology at the pachytene stage, in the sweet potato (*Ipomoea batatas* L.), which is a hexaploid ($2n = 90$), have thrown considerable light on its origin and genome relationships. Using suitable criteria, such as relative length of chromosomes, centromere position, chromomere pattern, absence of light staining segments in one of the arms, presence of telochromomere etc., 40 of the 45 haploid chromosome complement at pachytene were identified and assigned to 19 chromosomal types. Among these types, eight were present singly; in six of the types, chromosomes were present in duplicate, and in two types, in triplicate. The occurrence of higher multivalent chromosomal associations such as hexavalents and pentavalents, in addition to the quadrivalents already reported, was recorded for the first time at the pachytene and metaphase I stages. The hexavalents at pachytene were resolved into three distinct types based on the morphology of the participating chromosomes. A maximum number of nine quadrivalents at the metaphase I stage and four in the incompletely analyzed pachytene nuclei were recorded. The constituent chromosomes of three of the quadrivalents at pachytene stage were identified. From these observations, it is suggested that (i) the three parental genomes are partly homologous (ii) two of the genomes show closer homology to one another than to the third and (iii) the three genomes differ with respect to one or more of the eight chromosomal types occurring singly. The available information rules out an autopolyploid origin for sweet potato and suggests that the parental genomes are from closely related taxa. The advantages are emphasized of pursuing similar studies in other American *Ipomoea* species to unravel their relationship with the sweet potato. Among other meiotic irregularities, a translocated chromosome and a chromosome carrying inversion were detected at the pachytene stage and the possible role they may play in varietal differentiation is discussed.

*Ipomoea batatas* L., the sweet potato of commerce, is widely cultivated in the tropical and sub-tropical regions of both hemispheres for its calorie-rich, starchy tubers which are used as subsidiary food, livestock feed and raw material for starch industries. Because of its great economic importance, efforts are underway in various parts of the world to improve the crop through breeding programmes. The necessary cytogenetical information is also being sought by several workers (see Gustafsson and Gadd, 1965; Jones, 1968 for review). The available evidence clearly shows that the sweet potato is hexaploid ($2n = 90$) even though its origin is still obscure. An allohexaploid origin involving a tetraploid and diploid American species has been postulated (Gustafsson and Gadd, 1965). However, a resynthesis of sweet potato from its putative parent/parents is still to be made. The other possible ways of investigating its origin and of assessing the extent of homology of the constituent genomes have also been explored without success. For instance, genetical studies have failed to throw the necessary light on this problem. This is traceable to the complexity of the genetic systems, such as self- and cross-incompatibility, operating in this species; in addition the frequent occurrence of non-flowering types in $F_1$ and $F_2$ restricts the choice of parents in undertaking a comprehensive study involving parents representing wide genetic variability (JONES, 1967; WILLIAMS and COPE, 1967). Similarly, conventional cytological studies have also been handicapped by the very small size of the somatic chromosomes which range in length from 2.7 μ to 1.0 μ (SHARMA and DATTA, 1958). In the light of the success recently achieved in a diploid American species, *Ipomoea crassicaulis* (Krishnan, Magoon and Vijaya Bai, 1969), pachytene analysis was proposed, in spite of the high chromosome number. This paper reports the cytological evidence on the origin of sweet potato given by detailed karyological and chromosomal homology studies at pachytene.

## Material and Methods

The plants of a cultivar of *I. batatas* were vegetatively raised at the farm of the Institute. For the study of meiosis, buds of appropriate sizes were fixed in a mixture of one part of propionic acid and three parts of alcohol and stored at 4–10 °C. The smearing technique described by Swaminathan, Magoon and Mehra (1954) was adopted. The camera lucida drawings of pachytene chromosomes were made at a table magnification of × 1450 obtained from optical combinations of 7× eyepiece and 1:100, 1.30 apochromatic oil immersion objective. The chromosomes were identified using criteria such as relative length centromere position, chromomere pattern, distribution of dark- and light-staining regions and presence of telochromomere and nucleolar association. Post-pachytene stages were also critically studied. All the studies and photomicrographs were made from temporary preparations. However, a few slides were also made permanent adopting the procedure described by Bhaduri and Ghosh (1954).

## Observations

In the study of meiotic stages, the pachytene was analyzed in detail and several of the post-pachytene stages were also examined.

**Pachytene:** *Karyology*: Despite the high chromosome number, fairly good spreading of chromosomes could be achieved in many nuclei. However, the entire chromosomal complement could not be completely analyzed from one cell. The largest number of chromosomes of the haploid complement, 38, could be followed from end to end in a few cases (Fig. 1), while in several other nuclei, the number of analyzable chromosomes varied from 10 to 18 only. In all these nuclei chromosomal lengths ranged from 16.6 μ to 36.6 μ. They were differentially stained, the dark-staining regions occurring on either side of the centromere and the light-staining regions following the dark-staining regions distally. The dark-staining regions of many of the chromosomes offered reliable land marks as to the size, number and distribution of chromomeres by which these chromosomes could be identified. Additional characters used in chromosome identification included the presence of telochromomere and the absence of a distal light-staining region in one of the arms. The telochromomeric chromosomes were further characterized by their association with principal or accessory nucleoli. The chromosomes also differed in the location of the centromere, and three categories were recognized using arm-ratio differences, namely (i) 1:1.3 and less, (ii) 1:1.4 to 2.0 and (iii) 1:2.1 and above. Under these three categories, 40 of the total 45 haploid chromosomes of the complement identified so far were assigned to 19 chromosomal types.

Incorporating the mean cytological values for the chromosomes under the 19 chromosomal types, an ideogram was constructed (Fig. 13).

The salient features for identifying these types are detailed below:

A. Metacentric chromosomes, where on the basis of chromomeric pattern the following 8 chromosomal types are recognized.

Type (i): This is represented by one chromosome 23.4 μ in length. The diagnostic feature of this chromosome is the presence of a single macrochromomere in one of the arms. No other chromomeres are present in this chromosome.

Type (ii): A single chromosome is recognized in this type ranging in length from 24.8 μ to 25.7 μ. The dark-staining regions of the two arms represent in each a single chromomere and they are unequal in size.

Type (iii): Two chromosomes are known to belong to this type, which resembles type (ii) in having one chromomere in each of the arms, and differs in that the two chromomeres are of equal size; length varies from 20.0 μ to 27.6 μ.

Type (iv): This type is represented by two chromosomes ranging in length from 17.2 μ to 24.8 μ and is characterized by the presence of a distinct chromomere in one arm and a pair of chromomeres in the other arm.

Type (v): This is similar to the previous type in that it has one chromomere in one arm but differs in having a dark-staining segment in the other arm. The only chromosome recognized in this group varied in length from 20.7 μ to 31.0 μ.

Type (vi): This is distinguished by the presence of telochromomere in one of the arms but otherwise conforms in its general morphology to type (iii). A single chromosome with length of 25.5 μ is recognized under this type.

Type (vii): This is morphologically similar to type (v) except for the presence of telochromomere in the arm bearing one macrochromomere. The only chromosome of this type is 36.6 μ long.

Type (viii): The two chromosomes identified in this type are characterized by the presence of equal lengths of dark-staining segments in their arms, and range in length from 20.0 μ to 27 .6 μ.

B. Submetacentric chromosomes with arm ratio ranging from 1.4 to 2.0. Three chromosomal types are distinguished on the basis of chromomere pattern.

Type (i): It has four chromosomes carrying equal lengths of dark-staining segments. Lengths vary from 16.6 μ to 26.2 μ. In the shortest of the chromosomes in this group, the dark-staining segments of each of the arms could be resolved into three distinct chromomeres.

Type (ii): This is characterized by the distinct macrochromomere present in both the arms. The length of the single chromosome belonging to this group varies from 18.6 μ to 20.0 μ.

Type (iii): This contains two chromosomes, and is distinguished by the presence of a single chromomere in the short arm and two chromomeres in the long arm. The chromosomes range in length from 18.2 μ to 20.4 μ.

C. Acrocentric chromosomes with arm ratio ranging from 2.1 and above. It includes 8 chromosomal types.

Type (i): Three chromosomes varying in length from 23.4 μ to 26.2 μ are assigned to this group, which is recognized by the presence of a chromomere in each of the arms.

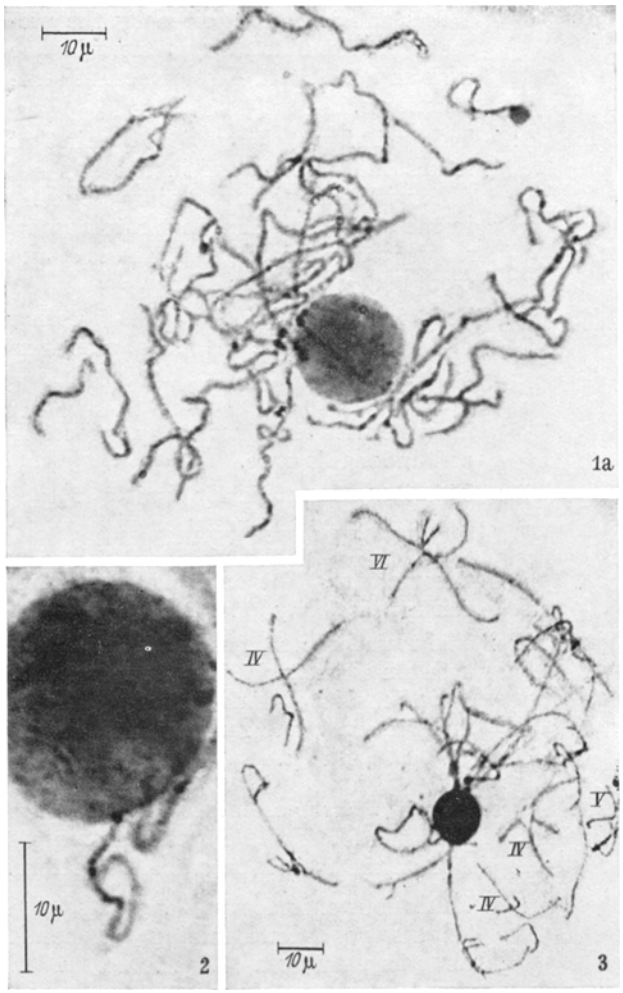


Fig. 1a. Pachytene nucleus showing differentiated chromosomes. Note the telochromomeric chromosome in association with accessory nucleolus (10 μ = 11 mm)

Fig. 2. Telochromomeric chromosome in association with principal nucleolus at pachytene (10 μ = 23 mm)

Fig. 3. Multivalent chromosomal associations at pachytene (10 μ = 8 mm)

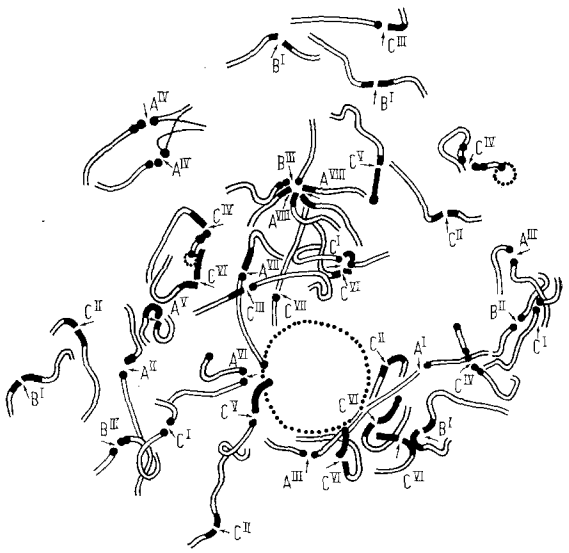

Fig. 1b. Interpretative drawing of Fig. 1a showing 18 of the 19 chromosomal types. Type C viii and one chromosome of type C vi are not distinguishable. Type C iii at 9 o'clock region being in different focus could not be included in Fig. 1a but is included in Fig. 1b; (10 μ = 11 mm)

Type (ii): This includes four chromosomes, ranging in length from 17.9 μ to 24.8 μ. The two arms possess approximately equal lengths of deep-staining segments.

Type (iii): This is represented by two chromosomes with lengths of 21.4 μ and 33.8 μ respectively, which have relatively longer dark-staining segments in the short arm.

Type (iv): This consists of three telochromomeric chromosomes varying in length from 20.5 μ to 24.1 μ. One of the chromosomes is associated with the principal nucleolus (Fig. 2) while the others are associated with accessory nucleolus (Fig. 1). As well as having telochromomere in the short arm, this type shows a distinct chromomere in the two arms in the immediate proximity of the centromere.

Type (v): This is characterized by a heteropycnotic short arm bearing a distinct telochromomere; the long arm of this type has a macrochromomere. There are two chromosomes ranging in length from 20.0 μ to 22.8 μ.

Type (vi): This is recognized by its heteropycnotic short arm and dark-staining segment in the long arm and is represented by six chromosomes ranging from 17.2 μ to 24.1 μ in length.

Type (vii): This is identified by the solitary chromomere in its short arm. The length of the only chromosome of this type is 22.8 μ.

Type (viii): It has two discrete macrochromomeres in the long arm and three medium to small chromomeres in the short arm. The only chromosome of this type is 20.7 μ long.

*Homology*: Extensive study was attempted of chromosomal pairing behaviour in a large number of nuclei. In no instance could the chromosomal association of the entire nucleus be worked out owing to the difficulties discussed earlier. However, the data available indicate that, in addition to the preponderance of bivalent chromosomal configurations, multivalent associations were also very common and occurred in 48 of the 51 incompletely analyzed nuclei. The multivalents were frequently quadrivalents rang-

ing from 1 to 4 and a hexavalent occurred in 33.3% cells. Pentavalents, numbering 1 or 2, were generally rare, accounting for only 4% of the cells. In one cell the maximum multivalent association consisting of 1 $^{VI}$, 1 $^{V}$, and 3 $^{IV}$ was observed (Fig. 3). The hexavalents observed in the present study could be assigned on the basis of their chromosomal morphology to one of the following three types. In the first type (Fig. 4) the participating chromosomes were acrocentric and were homomorphic in both their relative length and chromomere pattern. The second type of hexavalent included two pairs of homomorphic, metacentric chromosomes and a third acrocentric pair differing in its general morphology (Fig. 5). The third hexavalent type included 3 pairs of metacentric chromosomes of which one pair was morphologically dissimilar from the other two (Fig. 6). Pentavalent association was observed in two cases in both of which the separation of participating chromosomes was apparent. Because the measurement of unpaired segments, which are generally prone to greater stretching in the process of smearing, leads to conflicting observations, these pentavalents could not be analyzed in detail.

Among the quadrivalent chromosomal associations recognized in the various nuclei, three types could be distinguished on the basis of the morphology of the constituent chromosomes. The presence of other types, although conjectured on the basis of the relative lengths of participating chromosomes, could not be clearly established using the morphology of the chromosomes involved in the quadrivalent configuration. In the first of the three quadrivalent types the participating chromosomes belonged to type (iv) of 'A' category (Fig. 7), while in the second they consisted of chromosomal type (iii) of 'B' category. In the third type, the participation of chromosomal type (vi) of 'C' category could be demonstrated.

A few instances of aberrant chromosomal pairing were also observed. In one case this involved an interstitial inversion (Fig. 8), while in another a simple translocation in one of the homologues involving the terminal segment followed by reunion of the broken end to the other arm of the same chromosome was evident (Fig. 9).

*Diakinesis*: The study of chromosomal association at this stage was generally restricted to nucleolar chromosomes because in many cases the chromosomal configurations could not be clearly made out due to the pronounced condensation occurring in the chromosomes as they reach this stage. These studies have also shown multivalent association of nucleolus associated chromosomes (Fig. 10).

At *metaphase I* (Fig. 11), again the chromosomal association could not be reliably worked out for the entire nucleus in many instances. Thus, although a much larger number of cells at this stage were analyzed, the chromosomal associations of 28 cells were used to compute the frequency of various multivalents (Table 1). In 25% of the cells 1 or 2 hexavalents were noted, whereas nearly 97% of the cells had quadrivalents ranging from one to as high as nine.

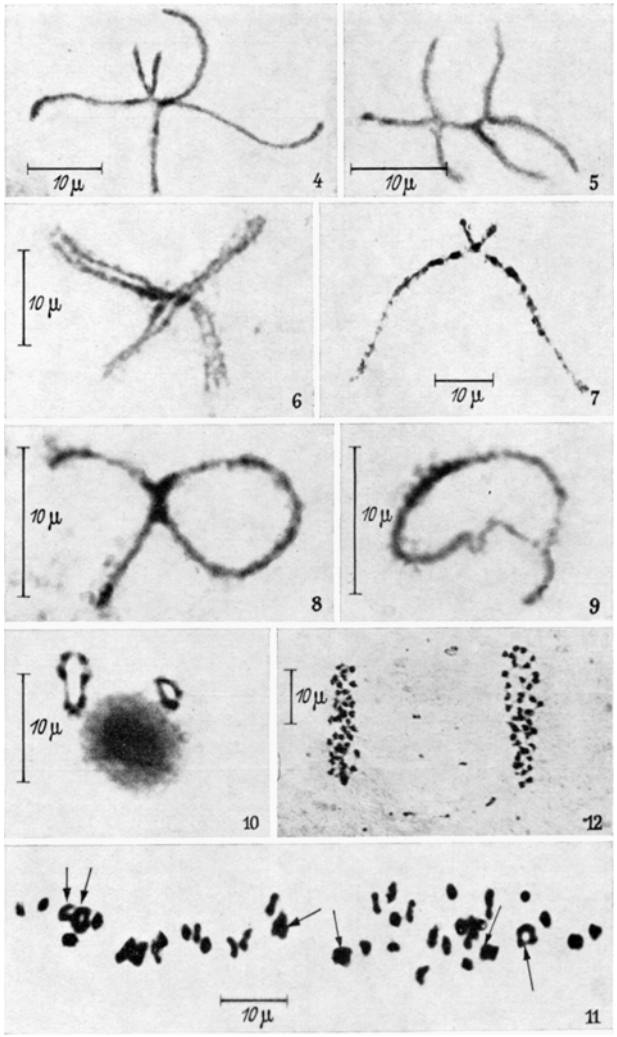


Fig. 4. Hexavalent association, type one, at pachytene (10 μ = 13 mm)

Fig. 5. Hexavalent association, type two, at pachytene (10 μ = 17 mm)

Fig. 6. Hexavalent association, type three, at pachytene (10 μ = 17 mm)

Fig. 7. Quadrivalent association at pachytene (10 μ = 10.5 mm)

Fig. 8. Inversion configuration in a pachytene bivalent (10 μ = 27 mm)

Fig. 9. Translocation configuration in a pachytene bivalent (10 μ = 27 mm)

Fig. 10. Multivalent configurations of nucleolus-associated chromosomes at diakinesis (10 μ = 19 mm)

Fig. 11. Quadrivalent chromosomal associations (arrows) at metaphase I (10 μ = 9 mm)

Fig. 12. Lagging chromosomes at anaphase I (10 μ = 12 mm)

Table 1. *Chromosomal associations at metaphase I*

| VI | V | IV | III | II | I | No. of cells analyzed |
|---|---|---|---|---|---|---|
| 1 | — | 3 | 1 | 34 | 1 | 1 |
| 1 | 1 | 8 | 1 | 21 | 2 | 1 |
| 1 | — | 7 | — | 28 | — | 1 |
| 1 | 1 | 5 | 1 | 26 | 4 | 1 |
| 1 | — | 5 | — | 32 | — | 2 |
| 2 | — | 4 | — | 31 | — | 1 |
| — | — | 3 | 1 | 37 | 1 | 3 |
| — | — | 3 | — | 38 | 2 | 1 |
| — | — | 1 | 1 | 40 | 3 | 1 |
| — | — | 4 | — | 37 | — | 1 |
| — | — | 5 | — | 35 | — | 1 |
| — | — | 7 | 1 | 29 | 1 | 1 |
| — | — | 3 | 2 | 36 | — | 1 |
| — | — | 7 | — | 30 | 2 | 2 |
| — | — | 9 | — | 26 | 2 | 1 |
| — | — | 6 | — | 32 | 2 | 2 |
| — | — | 1 | — | 42 | 2 | 1 |
| — | — | 3 | — | 39 | — | 1 |
| — | — | 1 | 1 | 41 | 1 | 1 |
| — | — | 6 | — | 33 | — | 1 |
| — | — | 2 | — | 40 | 2 | 1 |
| — | — | 5 | 1 | 33 | 1 | 1 |
| — | — | — | — | 45 | — | 1 |
| | | | | | Total | 28 |
| 0—2 | 0—1 | 0—9 | 0—2 | 21—45 | 0—4 | Range |
| 0.28 | 0.07 | 4.36 | 0.43 | 34.03 | 1.14 | Mean/cell |

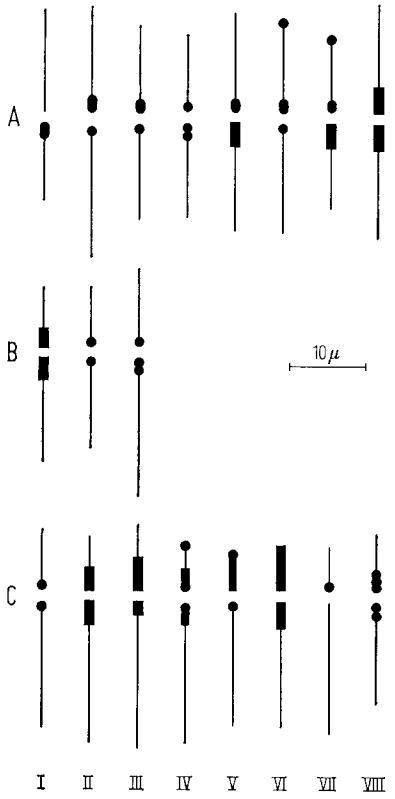


Fig. 13. Ideogram at pachytene showing the 19 chromosomal types; (10 μ = 14.5 mm)

Trivalent and pentavalent associations were relatively rare: the former, numbering 1 or 2, occurred in 33% of cells, while the latter, not exceeding one per cell, appeared in less than 7% of cells. Univalents were also few in number, ranging from 1 to 4, and occurred in 33.3% of cells. Bivalent associations ranged from 21 to 45. Among the multivalents, 3 and 5 quadrivalents per cell occurred frequently. Precocious movement of univalents to the poles occurred in metaphase I.

*Anaphase I and later stages*: Anaphase I chromosomal separation in this material was frequently irregular and characterized by laggards (Fig. 12) and bridge formation. Despite these irregularities, 83.8% of microspore tetrads did not contain any micronuclei, while in 9.4%, 6.3% and 0.5% of cells 1, 2 or 3 micronuclei, respectively, were recorded.

## Discussion

The origin of the sweet potato is still obscure. The predominantly bivalent synapsis of chromosomes at metaphase I reported by earlier workers (*vide* Gustafsson and Gadd, 1965 for review) has been one of the main criteria in postulating an allohexaploid origin. Added to the limited usefulness of such data in interpreting the origin of polyploids (cf. RILEY, 1960 for detailed discussion), there is the difficulty, inherent in conducting a critical study of this stage in sweet potato, of the minute size of its chromosomes and the high chromosome number. The small size of the chromosomes, however, proved to be a definite advantage in the karyological studies at pachytene because adequate chromosomal spreading could be achieved. Also, the differentiated pachytene chromosomes with their readily recognizable centromere and distinctive chromomere pattern allowed the consistent identification of chromosomes in almost all the analyzable pachytene nuclei. In the present discussion, the cytological evidence on the origin of sweet potato is examined on the basis of data from both karyology and chromosomal homology.

Pachytene analysis of sweet potato has brought to light more interesting information on the karyology of its constituent genomes than could be obtained by similar studies of somatic chromosomes. The study of somatic chromosomes at root-tip metaphase by Sharma and Datta (1958) proved unrewarding because of the small size of the chromosomes (range 1.0 —2.7 μ) and the paucity of adequate criteria — an inherent defect in the study of this stage. From these studies, the entire haploid complement could only be resolved into six types. On the other hand, the karyological studies at pachytene stage were very informative, in spite of the prohibitively high chromosome number of the taxus. The 40 of the 45 chromosomes of the haploid complement identified in the present study, have been placed into 19 types based on criteria such as arm ratio, chromomeric pattern,

nucleolar association etc. Among the 19 types, 8 types were found to be represented by a single chromosome, 6 types by two chromosomes each, 2 types by three and 2 types by four chromosomes, and a single type by six chromosomes. From chromosomal association studies, and taking into account the hexaploid nature of sweet potato, it may be interpreted that: (i) the eight chromosomal types present singly in the haploid complement are not represented in all the three genomes; (ii) the six types occurring in duplicate are common to two of the three genomes; (iii) the two types represented in triplicate are present in all the three genomes. Thus, the karyological observations suggest that all the parental genomes are karyologically distinguishable by one or more of the eight chromosomal types.

The multivalent chromosomal associations observed at pachytene and metaphase I stages show the prevalence of chromosomal homology among the constituent genomes. Although, at pachytene, only one hexavalent per cell was observed, the hexavalent association in various cells involved morphologically different chromosomal types which could be resolved into three distinct types based on their morphology. The first type consisted of homomorphic, acrocentric chromosomes that were evidently present in all three genomes. In the second type, chromosomes of only two of the genomes were homomorphic and metacentric, while that from the third genome was acrocentric, probably reflecting the chromosomal differentiation that had occurred in the latter genome. In the third hexavalent type, where all the participating chromosomes were metacentric, only two were similar in their chromomeric pattern.

The number of quadrivalents at metaphase I stage ranged from 1 to 9 and they were present in 27 of the total 28 cells studied. Even in the incompletely analyzed pachytene nuclei, the presence of as many as four quadrivalents could be demonstrated and quadrivalents occurred in 48 out of the 51 cells studied. Among the various quadrivalent chromosomal associations, three types were distinguishable on the basis of morphology. All three were found to involve homologous chromosomes and the specific types of the participating chromosomes have also been identified. The number of pentavalent chromosomal associations per cell at pachytene was 1 or 2, occurring in 4% of cells, while at metaphase I, 7% of cells had one pentavalent. However, the pentavalents at pachytene could not be critically studied with respect to the morphology of the constituent chromosomes because their lower frequency restricted the availability of suitably-stained preparations for analysis. The available evidence suggests the presence of as many as three chromosomes common to all the three parental genomes and an additional three chromosomal types common to two of the genomes.

Thus, the frequency of quadrivalent association (as high as nine at metaphase I), together with the occurrence of six chromosomal types in duplicate, suggests a closer homology between two of the three parental genomes. The third genome nevertheless shows some homology to the other two as is borne out by the occurrence of the three distinct hexavalent types. These results do not support the generally held theory of an allohexaploid origin for sweet potato (Gustafsson and Gadd, 1965) while the recognition of as many as 19 chromosomal types also rules out an autopolyploid origin from a single diploid progenitor. However, the available evidence can be interpreted as indicating the presence of three genomes of closely related taxa with marked chromosomal homology. The possible progenitors of sweet potato must be sought among the various diploid and tetraploid American species of *Ipomoea*, so pachytene analysis of these species would be very useful. In the hexaploid wild species, *I. trifida*, which is considered to be closely allied to sweet potato on morphological, cytological and genetical grounds, (Nishiyama, 1961; Nishiyama and Teramura, 1962) pachytene analysis would be worthwhile.

The present investigation confirmed the earlier observations of Jones (1965) and Ting and Kehr (1953) on the meiosis of sweet potato in that quadrivalent chromosomal association occurred. However, a higher frequency and number of quadrivalents were found than were reported by these workers.

As well as quadrivalent association, higher multivalent configurations including both hexavalents and pentavalents were also recognized for the first time at both pachytene and metaphase I stages. The apparent contradiction in the meiotic behaviour of sweet potato in the present and previous investigations may be partly due to the limitations imposed by the highly condensed chromosomes at diakinesis and metaphase I stages. The higher chromosome number of this taxon also contributes to this difficulty.

Ting, Kehr and Miller (1957) reported the secondary association of bivalents at MI in sweet potato and this has been considered as "possibly suggesting a general affinity of corresponding chromosome pairs" (Gustafsson and Gadd, 1965). In the present investigation, however, secondary association of chromosomes was not discernible even at the earlier prophase stages. Furthermore, interpreting the origin of polyploids, especially the so-called secondary polyploids, on this basis has been disputed because of the unequivocal nature of the conclusions drawn from these observations. There are differences of opinion on the real significance of secondary pairing of chromosomes. Factors other than ancestral homology have been implicated as being responsible for this phenomenon (see for review, Magoon, Cooper and Hougas, 1958 and Magoon and Ramanujam, 1960). From the available evidence, Stebbins (1950), Magoon, Ramanujam and Cooper (1962), and Swaminathan and Magoon (1961) have concluded that, although secondary association can be considered to

be a real phenomenon and one which in certain cases suggests the polyploid nature of a species or genus, it is liable to be considerably modified by segmental interchange, duplication of chromosome segments and other phenomena not-at-all related to polyploidy. It is therefore not a reliable index of the exact basic number possessed by the original ancestors of a group. It would appear that a cautious approach is necessary in using this evidence either to derive the basic chromosome number of the genus or to show residual affinity between chromosomes which are phylogenetically or ancestrally related.

Among the various chromosomal types recognized at pachytene in the present investigation, the telochromomeric chromosome stands out by virtue of its distinct morphology and frequent association with principal or accessory nucleoli. The telochromomeres are borne in one of the arms and when present in the acrocentric chromosome are located in the short arm. Among the five telochromomeric chromosomes identified so far, three are acrocentric and are morphologically similar. The remaining two are metacentric and are distinct with reference to the chromomere pattern of the telochromomere-lacking arm only. Thus, the five telochromomeric chromosomes could be broadly divided into two groups based on centromere position. The presence of both chromosomal types in the diploid progenitors of sweet potato could be postulated, in the light of our knowledge on the pachytene karyology of an American diploid species, *I. crassicaulis* (Krishnan, Magoon and Vijaya Bai, 1969). In this species also, the two nucleolar chromosomes bear terminal organizers in one of the arms comparable in size to the telochromomeres and the chromosomes are distinguishable by their relative length.

The pachytene analysis has also thrown light on the chromosomal differentiation that has occurred and been preserved in the sweet potato, which is known to have been in cultivation for over 5000 years (see Gustafsson and Gadd, 1965). Two instances of aberrant pairing were noted, in one case involving a simple translocation of the terminal segment in one arm and its subsequent reunion with the other arm, and in the other case, an interstitial inversion. Because such spontaneous chromosomal aberrations are easily preserved in the vegetatively propagated species, they could contribute to further chromosomal differentiation of the various cultivars.

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