CYTOLOGICAL STUDIES IN THE GENUS IPOMOEA AND RELATED GENERA

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Introduction

The solution to many problems in taxonomy, genetics, and evolution has been sought by a study of chromosomes. Special importance has been attached to the number, structure, and behavior of the chromosomes in this relation. During the past few years this tendency has been popular with reference to many economic plants, especially to determine their relationship to other members of the same and related genera by means of the chromosomes, with the hope of improving them. The genus Ipomoea presented such an opportunity. The relationship of the sweet potato, I. batatas, and other members of this genus suggested a very interesting study; while the flowers were favorable for hybridization. The fact that only six species have been investigated cytologically made possible an almost unlimited study of the genus. In view of this, the problem was approached

with four principal objectives in mind: (1) to determine the chromosome numbers of as many species and varieties as possible; (2) to examine the pollen in the same; and (3) to attempt interspecific and intergeneric hybridization among these forms, and to study the chromosomes in the hydrids obtained.

Literature Review

The results of chromosome studies in many genera show that the relation of the chromosomes to problems of taxonomy seem to be generally correlated with that of number; while in problems of genetics, it is one of structure and behavior. The relation of chromosomes to evolution includes each of these. In view of this, it is evident that such studies are, themselves, closely related, since they are all somehow related to the activities and the characteristics of the chromosomes.

Although it has been known for some time (Gates, 1925) (Hurst, 1932) that related species, and even genera, differ from each other not only in chromosome number but also in size and shape, the first of these differences to be knownwas the former. The work on the determinations of chromosome numbers shows that they tend to fall within

certain arbitrary categories of classification. A thorough study of the monographs on chromosome numbers (Gaiser, 1926, 1930a, 1930b,1933) and the recent texts will reveal the fact that plants generally may be classified taxonomically, to a certain extent, according to the chromosome number existing in the species and varieties of each genus. A knowledge of the chromosome number is an important element in the classification of that form taxonomically and in its determination phylogenetically (Ostenfeld, 1925). The relation existing in some genera between the chromosome numbers and the taxonomy of the group may best be seen in Rosa, Triticum, Viola, Gossypium, and Fragaria.

The great advances in genetics have also been attained through a knowledge of chromosomes, not especially, however, with reference to their numbers, but rather to their structure and behavior. This may well be seen in the extensive investigations in Datura, Oenothera, and Zea.

The problem of the origin of species, or phylogeny, it seems, should be dealt with separately in each genus; since the group characteristics will vary (Babcock, 1931); and some factors operating in these changes will be manifest to a greater or lesser extent in one genus than in another. These phylogenetic considerations, although involving in most cases both chromosome structure and behavior, are based primarily upon a knowledge of chromosome numbers.

The wide-spread occurrence of polypoidy and its role in the appearance of new characters in plant forms, as shown by experimental evidence, makes it a strong factor in the species concept and in the phylogeny of some genera.

It is obviously impossible and impractical to give a complete review of the voluminous literature which has appeared on the subject of chromosome numbers in all plant genera. An attempt will be made, however, to review briefly the chromosome number relationships within those more thoroughly investigated; or to point out polypoidy, aneuploidy, and homoploidy as they exist in related species or varieties within other genera.

In the majority of genera investigated, the chromosome numbers in the various species form a multiple series. For example, in Rosa (Blackburn and Harrison, 1921) (Tackholm, 1922) (Hurst, 1925) (Blackburn, 1925) (Erlanson, 1929, 1930, 1931) the various species have 14, 21, 28, 35, 42, 49, and 56 somatic chromosomes; hence they range from diploid to octoploid, with 7 as the fundamental number. In Potentilla (Shimotomai, 1930), a condition similar to that in Rosa is present, except that the gametic numbers form the series, 7, 14, 21, 28, 35, 42, 49, and 56. In Draba (Heilborn, 1927), with a basic number of 8, the species range from diploid to hexaploid; and in Pelargonium, from diploid

to decaploid (Takagi, 1928).

Such long unbroken polyploid series are rather rare, but series with two to four numbers are very common, and may be found in such genera as Rubus (Longley, 1923, 1924a, 1924b) Crataegus (Longley, 1923, 1924a, 1924b), Gossypium (Denham,1924), Fragaria (Longley, 1926), Triticum (Aase & Powers, 1926), Petunia (Dermen, 1930), Lonicera (Sax & Kribs, 1930), Sedum (Baldwin, 1935), the Gramineae (Church, 1929), the Cactaceae (Stockwell, 1935), and many others.

Taxonomic relationships with chromosome numbers is indicated within some genera. Among the well known examples is that of Triticum, wherein the Einkorn group has 7 chromosomes, the Emmer group, 14 chromosomes, and the Vulgare group, 21 chromosomes; while in Gossypium, the American species have 26 somatic chromosomes and the European, or Asiatic, species have 13 somatic chromosomes. Other equally familiar examples are those of Rosa and Viola where, for the most part, species belonging to the same sections have similar chromosome numbers.

Frequently a genus shows two multiple series of chromosome numbers, as in Papaver (Ljungdahl, 1922), Anemone and Ranunculus (Langlet, 1927) (Larter, 1932); and Trifolium (Kawakami, 1930); or even a three series, as has been found in Viola (Clausen, 1927) (Miyaji, 1930).

These series are usually short, as shown by the 14,28, 48, and 8, 16, 32 series in both Anemone and Ranunculus; while Papaver has a 7, 14, 21, 35, and a 11, 22 series; and Trifolium, the two series of 8, 12, 16, 2n-48, and 7, 14. The three groups in Viola are formed respectively upon the basic numbers 6, 10, and 12.

Another condition often present in a genus is that in which polyploidy may be combined with aneuploidy. Thus in Crepis (Babcock & Navaschin, 1930), the thirteen different numbers (6, 8, 10, 12, 14, 15, 16, 22, 33, 40, 44, 55, and 88) represent a short multiple series with a basic number of 11, together with non-multiple numbers. In Rumex, (Kihara & Ono, 1926) the species of the Eulapathum section show gametic numbers of 10, 20, 30, 40, 50, 60, and 100; while those of the Acetosa section show 4, 7, 8, 10, and 21. In Primula (Bruun, 1932) the somatic numbers (16, 18, 20, 22, 24, 36, 40, 42, 44, 48, 52, 54, 56, 64, 72, 90, and 126) are likewise in both polyploid and aneuploid relation. Similar conditions are found in Datura (Blakeslee, 1922), Prunus (Okabe, 1928), Iris (Longley, 1928) (Kazoa, 1928) Betula (Woodworth, 1929), Oenothera (Cleland, 1929 and others), and the Cruciferae (Manton, 1932).

The chromosome numbers in some genera, instead of forming multiple series, bear an irregular relation to

each other. Striking examples of such an aneuploid condition within a genus is afforded by Carex (Heilborn, 1924) in which the species examined show 22 different gametic numbers, all of which lie between 9 and 56; and Scirpus (Hicks,1928), whose irregular series include the numbers 18, 20, 21, 25-30, 28, 33, 34,38,39,50-64, 53-55, 55,55-57. These represent the extreme, and are uncommon, but many less striking examples are found, such as Nicotiana (Goodspeed, 1933) with the numbers 9,10,12, 16,20,22, 24, and 32; and the four taxonomically stable genera of the Cyperaceae (Cyperus, Eleocharis, Dulichium, and Eriophorum) (Hicks, 1929). In Medicago (Fryer, 1930), Linum (Martzentzina, 1927), Crocus (Brittingham, 1932), the Diantheae (Blackburn, 1927), and other genera, aneuploidy is present to a less degree.

The origin of new types in genera containing such irregular chromosome relations has probably occurred through hybridization, adcompanied by chromosome irregularities.

In contrast with polyploid and aneuploid genera, wherein numerical chromosome changes occur, are the homoploid genera, such a Philadelphus (Bangham, 1929), all of whose investigated species have 3 gametic chromosomes; Arachis (Husted, 1931, 1933) with 40 somatic chromosomes

in all of the forms; Lilium (Gaiser's rev., 1930b) with 12 gametic chromosomes; Epilobium (Johansen, 1929) with 36 somatic chromosomes; and the Conifers (Sax & Sax,1933) in which each genus has a constant chromosome number among the species; the most common number being 12. Other genera, such as Tilia (Dermen, 1932),with 41 gametic chromosomes; Mahonia and Berberis (Dermen, 1931) with 14 pairs; Ficus (Condit, 1933) with 13 gametic chromosomes; the Leguminoseae (Kawakami, 1930) with 8 to 12; and Lathyrus, Ervum, and Pisum (Sveshnikova, 1927) with 7 show a similar homoploid condition. Equally significant are several extensively investigated genera whose chromosome numbers, with a few exceptions, form a homoploid series. Here are included Anthurium (Gaiser, 1927), Rhododendron (Sax, 1930) (Nakamura, 1931), Dahlia (Ishikawa, 1911), Pyrus (Nebel, 1929), Vitis (Sax, 1929) (Nebel, 1928), Silene (Blackburn, 1927), Lychnis (Blackburn, 1927) and Sambucus (Sax & Kribs, 1932).

Irregularities in chromosome number relations

Heteroploidy occurs not only between related species in a genus, but also between genera within a family, between members within a species, and even within an individual itself.

Related genera often show related chromosome numbers. In the Magnoliales (Whitaker, 1933), the genera may be arranged into two groups, one with a basic number of 14, and the other with a basic number of 19. In the Cruciferae (Manton, 1932), an aneuploid relation exists between fundamental numbers of the genera, such as 5, 6, 7, 8, 11, 13, and 15. In contrast to this, the basic numbers of genera of the Capridifoliaceae (Gaiser's rev., 1933) form a polyploid series of 9, 18, 27. Several series of chromosome numbers exist among the genera of the different families in the Bicornes (Wanscher, 1934).

Individuals or races within a species often differ in chromosome number, as in Silene ciliata (Blackburn, 1933) with two subspecies, each exhibiting polyploidy, and two strains, which are similar externally, yet one having a gametic chromosome number of 24, and the other, a gametic number of 96; Prunus laurocerasus (Meurman, 1929) with a 22-ploid form; Festuca elatior and F. ovina (Levitsky & Kuzmina, 1927) in each of which is present the polyploid series, 14, 28, 42, and 70, involving subspecies, varieties, and subvarieties; Viola canina (Bruun, 1932) whose chromosome number varies from 36 to 40; Prunus serrulata (Okabe, 1928) with 16, 24 and 25 chromosome races; and the 2n-plus-1 forms in Datura (Blakeslee, 1922). Other cases of heteroploidy within a

species may be cited in Salix triandra (Blackburn & Harrison, 1924); Secale cereale (Emme, 1927); Zea Mays (Humphrey, 1933); and Medicato falcata (Fryer, 1930). These serve to indicate that this condition is rather common in plant forms.

Very often, one area, or even a single cell, may differ from the remainder in chromosome number. Somatic doubling is common in the root tips of Ranunculus (Larter, 1932), while in the Onograceae (Johansen, 1929), the chromosome number will vary widely in the different tissues of the same plant, or two different chromosome series (n-7, 2n-14; and n-9, 2n-18) may occur in the same plant. In Solanum Lycopersicum (Huskins, 1932) triploid shoots have arisen from callus tissue. In Sorghum (Huskins & Smith, 1932), Nicotiana silvestris (Webber, 1930), and in four species of Medicago (Fryer, 1930), polyploid areas (usually tetraploid chimeras) have been found.

Such heteroploid areas or individual cells are believed to be associated with the origin of shoots or roots having irregular chromosome numbers.

The results of chromosome studies in the Convolvulaceae by other workers is presented in Table I.

Material and Methods

The supply of seeds of the species and varieties of Ipomoea Quamoclit, Calonyction, Operculina, and Merremia (species of the latter four genera are many times known commercially as species of Ipomoea)were procured from various seed firms and from collectors in the United States, Central and South America, and Europe. The roots of the varieties of I. batatas were secured from the United States Department of Agriculture; while flower buds of some varieties were received from Porto Rico through the kindness of Dr. B. F. Lutman. A monograph (House, 1908) on the North American Ipomoea, that includes 175 species, was used in determining the members of this genus. Many duplications, resulting from the commercial names, made this monograph a very valuable aid. House (1906, 1909), likewise is referred to in the determination of the species in Quamoclit and Operculina. The collection of specimens in the National Herbarium in Washington was also consulted.

The roots of the varieties of I. batatas and the seeds of the other species were grown in the greenhouse.

The seeds were first nicked with a file, and soaked in water for several hours. Several plants of all species but I. batatas were transplanted to the field, while the remaining, including the sweet potato varieties, were used for the collection of root tips. Such material of I. pandurata was obtained from plants growing in the field.

Root tips were used for the determination of the somatic number of chromosomes. Several fixatives were used for this -- Flemming's Medium, Allen's modification of Bouin's Fluid, and Navachin's Fluid. Flemming's Medium was found to give the best results. Fixations were made between 8 A.M. and 5 P.M.; but the time apparently had little to do with the percentage of mitotic figures present.

The preparation of the flower buds presented a problem. The fixatives first used--Allen's modification of Bouin's Fluid, Dermen's Fluid, and Flemming's Medium--caused so much skrinkage, shriveling, and distortion of the pollen mother cells at the critical stages that the material was useless. The use of the smear technique (Belling, 1921) with fresh material, and also after fixation with Carnoy's Fluid, met with little success. A few flower buds of the fresh material, however, gave satisfactory results. On the other hand, a modified Navaschin's Fluid gave better

fixation, especially when the flower buds were placed in a vacuum for twenty minutes.

Both flower buds and root tips were carried through the alcohol-xylol-paraffin series; and the sections cut 10-13 microns. Great thicknesses of the sections in Quamoclit (Kagawa & Nakajima, 1933) and Pharbitis (U, 1930) (17-25 microns) gave the best results.

The presence of this fixative many times caused a clumping of the chromosomes in the first division (Figs. 43,44), but the prophase (Figs. 28 and 45) and the second division were preserved better, and splendid figures of all stages of this division were present. Chromosome number determinations, therefore, were made mostly from the metaphase of the second division (Fig. 27). In temporary aceto-carmine mounts of flower buds of the dicots, the second metaphase has been found to be the best stage for the counting of chromosomes (Belling, 1921).

The best time for the fixation of the meiotic division in Pharbitis nil (U, 1930) is between 3 P.M. and 5 P.M.; while buds fixed in the morning hours contained pollen mother cells mostly in the prophase, anaphase, and interphase stages. In Ipomoea, there

appeared to be no relation between the time of day and the stages of meiosis. The failure of some species to flower in this region made the collection of these impossible in some cases. All of the sections were stained with iron alum-hematoxylin.

Pollen germination tests were made in cane sugar solutions and in distilled water, by the hanging drop method. Small quantities of pollen were placed in different concentrations of sugar, ranging from 5% to 40%, and in distilled water, both at room temperature and in a constant temperature oven at 25 degrees Centigrade. Permanent slide mounts of pollen were made in thin balsam.

The Convolvulaceae are very favorable for artificial pollination because of the long style, large anther, the tubular corolla, the usually large size of the flower, and also the annual type of plant. During the first part of the hybridization work, the castrated and pollinated flowers were covered with paper bags or cellophane wrappers. Later, however, the work of cobbon (Doak, 1934) suggested a more convenient method. Instead of the clumsy paper or cellophane bag covering the entire flower, a short segment of a soda straw, open only at one end, was placed over the pistil of the receptive flower. The tubular corolla, whose furled

tip had been clipped off and stamens removed, was then firmly drawn to the straw with a piece of string, so that the flower was closed and the pistil further protected from insects by the soda straw. Very small flowers, such as those of I.lacunosa, were placed entirely within the soda straw; and the open end of the straw, which had been slit several times, was drawn together with string. In pollination, the stigma could be quickly exposed by removing the straw. Pollination was accomplished either by rubbing the anther on the stigma, or by collecting pollen on a needle and transferring it. The collections of seeds were made in September and October.

Results

Chromosome numbers

In the following table are given the chromosome numbers of the sixty-four species, varieties, and hybrids studied in Ipomoea, Quamoclit, Calonyction, Operculina, and Merremia. (Illustrations of chromosome configurations in representative forms are presented in Figures 1 to 26.)

species or variety	n	2n	determined by
Ipomoea			
Orthipomoea			
Leptophyllae			
leptophylla Torr.		30	King
Arborescentes			
arborescens (Humb.& Bonpl.) G. Don		30	King
Pharbitis			
Cephalanthae			
ruber (Vahl.) Millsp.		30	King
Hederaceae			
purpurea (L.) Lam.			
var.striped violet		30	King
white-with red throat		30	"
black-blue		30	"
carmine	15	30	"
.striped red		30	"
spotted violet		30	"
rose		30	"
lilac		30	"
light blue		30	"
double-semidouble	15	30	"
white		30	"
hederacea (L.) Jacq.		30	"
	15		Kano,1929.
var.Imperialis	15	30	King
Imp. Jap. purple		30	"
Imp. Jap. white	15	30	"
Imp. Jap. mottled	15	30	"
Giant Jap.		30	"
Japonica viridifolia	15	30	"
nil (L. in part) Roth		30	",Nagao,1928
	15		Kano,1929.
	12-14		Yasui,1928.
		24-28	Ogha,1916
learii Paxton		30	King
Batatas			
Erpipomoea			
pes-caprae (L.)Roth		30	King
setosa Ker.	15	30	"
Palmatae			
cairica (L.) Sweet.		30	"
digitata L.	15	30	"
Jalapae			
pandurata (L.) G.F.W. Mey	15	30	"

species or variety	n	2n	determined by
Emeticae			
purga (Wneder.)Hayne.		24-28	Heitz, 1926.
Aequisepalae			
ramoni Choisy.		60	King
lacunosa L.	15	30	"
var. white	15	30	"
purple	15	30	"
Sibirica	15		"
batatas			
var. White Sport		ca.90	"
Big Stem Jersey		ca.90	"
Nancy Hall		ca.90	"
Key West		ca.90	"
Porto Rico		ca.90	"
Seedling 169-3		ca.90	"
Seedling 259		ca.90?	"
Seedling 24171		ca.90	"
Seedling 312		ca.90	"
Vineland Bush		ca.90	"
violacea L.(rubrocoerulea)		30	"
var. Baby Blue	15	30	"
violacea vera		30	"
Quamoclit			
coccinea hederifolia(L.) House	14	28	King,Kagawa & Nakajima,1933.
coccinea (L.) Moench.		28	King, Kagawa & Nakajima, 1933.
	15		Kano, 1929.
pinnata (Desr.) Boj.			
var. red		30	King,Kagawa & Nakajima,1933.
white	15	30	King
		30	Kagawa & Nakajima, 1933.
pink		30	King
Sloteri		58	King,Kagawa & Nakajima,1933.
	30		Kano,1929.
lebata (Llav. & Lex.)		28	King
vulgaris	15		Kano,1929.
Operculina			
tuberosa Meissn.		30	King
dissecta House.		30	"

species or variety	n	2n	determined by
Calonyction			
aculeatum (L.)House		30	King, Nakajima, 1931.
(bona nox, grandiflora)			Kano, 1929
var.-Christmas Vine	15	30	King
Merremia			
distillatoria (Blanco.)(?)		30(?)	King
Calystegia			
Soldanella	11		Kano, 1929
sepium var. Japonica	11		Kano, 1929
Convolvus (Convolvulus)			
tricolor		30	Heitz, 1926, Kano, 1929
elongatus		22	Heitz, 1926
scammonia		ca.24	Heitz, 1926
undulatus		22-24	" 1926
siculus		44	" 1926
Unclassified			
Ipomoea obscura	15	30	King
Giant Pink (I.mexicana?)		30	"
Quamoclit scarletina		28	"
Quamoclit species (3)		28,30,58	Kano, 1929
Ipomoea species		30	Kano, 1929
Pharbitis (Ipomoea) nil		15	U , 1930.
haploid			
Ipomoea purpurea var.	15		Kano, 1925
Ipomoea batatas var.	42?		Kano, 1926
Q.angulata X Q.pennata red		29	Kagawa & Nakajima, 1933
Q.angulata X Q.pennata white		29	Kagawa & Nakajima, 1933
			King, Nohara, 1930?
Q.coccinea hederifolia X Q. pennata red		29	Kagawa & Nakajima, 1933
Q.coccinea hederifolia X Q. pennata white		29	Kagawa & Nakajima, 1933
Q.Sloteri X Q. coccinea			Nohara, 1930.
Q.coccinea hederifolia X Q. coccinea (reciprocal)		28	King

species or variety	n	2n	determined by
Q.pinnata red X Q.pinnata white			Nohara, 1930.
I.batatas X I. fastigiata			Tioutine, 1935
I.batatas X I. macrorhiza			Tioutine, 1935
I.batatas X I.pandurata			Tioutine,1935
Crosses among I. batatas varieties			Tioutine, 1935

Pollen

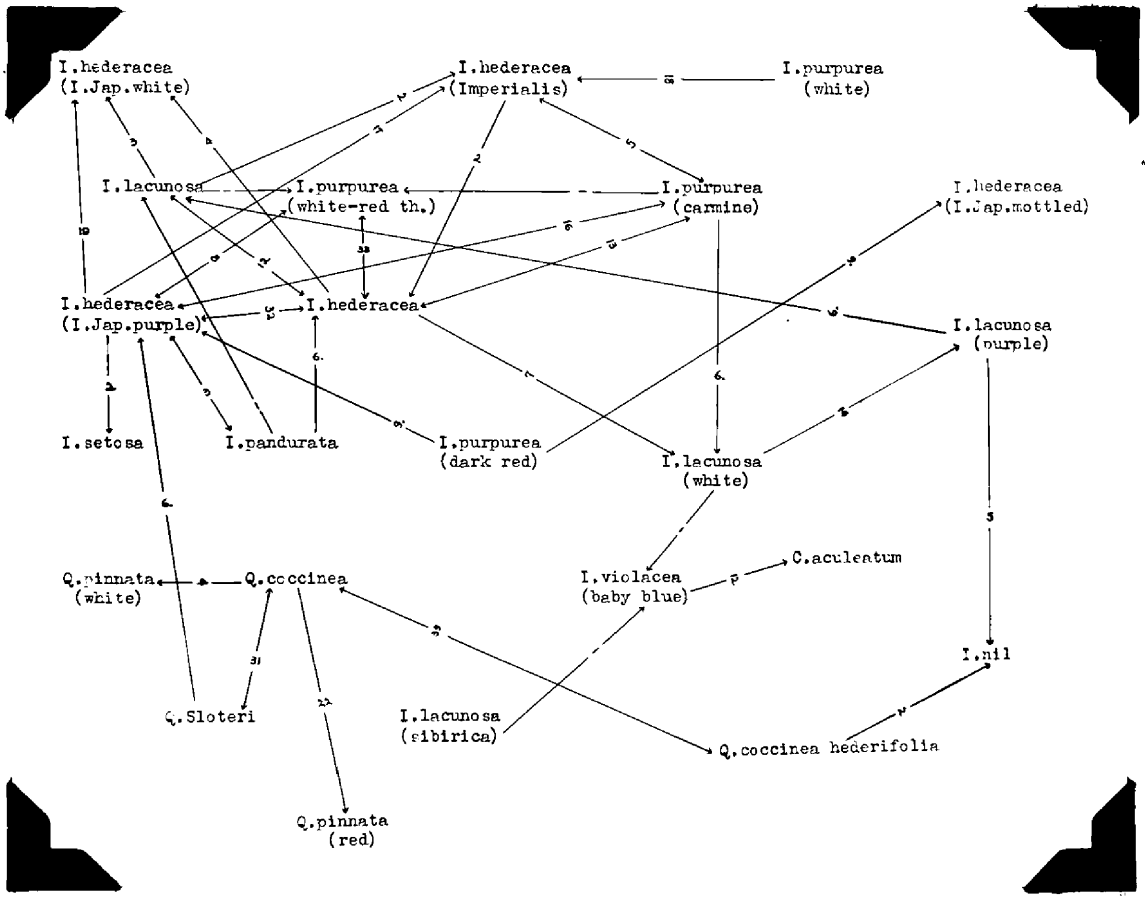
The studies on pollen, which were carried on for three years consisted of the examination of permanent pollen mounts and the germination of pollen in sugar solutions. These two studies were made in view of determining the relation between morphologically perfect pollen and functional pollen, and of comparing such pollen with that of hybrids.

The pollen of all of the species and varieties of Ipomoea, Quamoclit, Calonyction, Operculina, and Merremia appeared to be morphologically perfect. The only imperfect group of pollen was that of the hybrid Quamoclit pinnata (white) X Q. coccinea, when compared with that of its parents (Figs. 37, 38, 39). The pollen of the reciprocal hybrids of the cross Q. coccinea hederifolia X Q. coccinea

however, was similar to that of its parents (Figs. 39, 40,41).

Hybridization

The following chart includes the various crosses made in the hybridization studies:



The crosses, although limited because of the failure of some of the plants to flower, included interspecific (between closely and more distantly related species), intervarietal, and intergeneric combinations; involving both similar and different chromosome numbers. Only three crosses were successful: Quamoclit pinnata (white) X Q. coccinea, and the reciprocal crosses between Q. coccinea hederifolia and Q. coccinea.

Discussion

Chromosome Numbers

The study of only ten species of the four genera Quamoclit, Operculina, Calonyction, and Merremia does not warrant their inclusion in a discussion of the more thoroughly investigated genus, Ipomoea. It is of significance, however, that most of these representative species have 30 chromosomes. A condition comparable to that in Ipomoea may exist within each genus; but to state that such is present, is impossible at this time. In certain other families, a polyploid, aneuploid, or homoploid relationship exists between the genera, as in the Leguminoseae (Kawakami, 1930), Ranunculaceae

(Langlet, 1927), Caryophyllaceae (Gaiser's rev. 1926, 1930a,1930b, 1933), Scrophylariaceae (Gaiser's rev., 1926, 1930a, 1930b, 1933), and the Ulmaceae (Sax, 1933).

The relatively large number of representative forms studied in Ipomoea permits it to be included with the small group of genera in which a large number of forms have been investigated, and found to possess a constant chromosome number in every, or nearly every, species and variety, such as Anthrium, Philadelphus, Rhododendron, Lilium, the Conifers, and others. This seems to indicate that the origin of new forms has involved, for the most part, no change in chromosome number. In Anthurium (Gaiser, 1927), hybridization results in no great disturbances, either qualitative or quantitative, in the chromosomes; so that variation has arisen with little divergence in the chromosome number. The constant chromosome number in Philadelphus, Ficus, and Rhododendron, and the wide geographically separated species seem to indicate that the origin of new forms has been accompanied by no numerical change in the chromosomes. A comparable condition existing between the genera Mahonia and Berberis (Dermen, 1931) and among the species of each genus leads to the belief that they are of common origin.

The role of chromosomes in the phylogeny of a homoploid genus has, perhaps, not been quantitative, but rather a qualitative change within the individual chromosomes themselves. This also seems evident in other genera, as Primula (Bruun, 1932), Penstemon (Winge, 1925), and Crepis (Babcock & Navaschin, 1930).

In polyploid and aneuploid genera, the presence of high chromosome numbers is, in most cases, associated with hybridization. This can best be illustrated in such genera as Rosa, Triticum, Potentilla, Gossypium, Crepis, Primula, Iris, Scirpus, and others, in which hybridization, if present, is usually accompanied by a numerical change in the chromosomes. In the homoploid genera, however, this is the exception rather than the rule. Such seems to be true in the two polyploid forms, Anthurium crassinervium and A. digitatum (Gaiser, 1927), since it is possible that they are the result of hybridization followed by a doubling of the chromosomes.

A similar condition for Ipomoea batatas and I. ramoni is evidenced by the presence of natural hybridization among the sweet potato varieties in the Virgin Islands (Thompson, 1925), by the recent production of flowering hybrids in Russia from crosses between sweet potato varieties from Java, Formosa, Hawaii, Bermuda and the United States (Tioutine, 1935), and by the presence of Quamoclit Sloteri,

whose probable origin will be discussed later.

Two possibilities, in general, have been suggested for the origin of I. batatas (Tioutine, 1935). A New World origin from I. fastigiata, an edible tropical American tuberous form, known as "wild potato" in Jamaica and as "wild sweet potato" in Martinique and Quadeloupe, is supported by the taxonomic position of the two forms and by hybridization studies between tuberous species of the genus. In crosses between I. batatas, I. macrorhiza, I.fastigiata, and I.pandurata, the greatest success was attained in the I. batatas X I. fastigiata combination (Tioutine, 1935). From this, it is assumed that the generic relation between I. batatas and I. fastigiata is closer than between each of them and any other species of the genus. An Old World origin has been sought in I. mammosa, a native of Abouana and cultivated in Indo-China.

The diploid chromosome number of 60 for I. ramoni (Figs. 5,29) suggests that it may have arisen through the reduplication of the entire diploid complement, resulting in the tetraploid condition (amphidiploidy); which may, or may not, have followed hybridization. In the course of such processes, it is possible that the 90 chromosome condition in the varieties of I. batatas may have arisen later through hybridization between a 30 chromosome form and a 60 chromosome form, followed by reduplication of the

45 somatic chromosomes of the hybrid. This would result in a hexaploid form with 90 chromosomes, which would be fertile. The presence and importance of such an amphidiploid condition in the phylogeny of other genera as Nicotiana (Goodspeed, 1933) Crepis (Babcock & Navaschin, 1930) and many others is becoming more evident. This consideration of the origin of the 90 chromosomes would make I. batatas phylogenetically of more recent origin in respect to the other species in the genus. Such a view is considered in Viola (Gershoy, 1928) and in Potentilla (Shimotomai, 1930), where it is assumed that those species with low chromosome numbers, few variads, and wide geographical distribution are nearest their phylogenetic ancestors; while those with higher chromosome numbers and large number of variads are considered to be of more recent origin. The wide range of I. batatas must be contributed, at least in part, to its economic use.

It is possible, therefore, that there is represented in Ipomoea the chromosome numbers of one polyploid series, with a basic number of 15; and that I. batatas and I. ramoni are related cytologically to the other species of the genus through the course of hybridization,

together with chromosome reduplication. This should in no way conflict with the homoploid state of the genus.

The constant chromosome number in the varieties of Ipomoea purpurea, I. batatas, I. hederacea, and I. lacunosa raises the question as to whether that which is called a variety in one genus is comparable to that which is called a race or even a species in another genus. A similar homoploid condition is present in the somatic number of 40 for seven varieties of Cucurbita Pepo and three varieties of C. Moschata (Ruttle, Mrs. Nebel, 1931); the 40 somatic chromosomes of sixteen commercial varieties of Arachis hypogaea (Husted, 1931, 1933); and the 14 somatic chromosomes of fifty-seven varieties from twenty-eight forms of Phlox (Flory, 1931, 1934). In contrast to such homoploidy among varieties, Prunus serrulata contains races with 16, 24, and 25 chromosomes respectively; while the chromosome numbers in varieties of Pyrus form the polyploid series of 17, 34, and 51 (Nebel, 1930). In the Saretha group of Saccharum (Bremer, 1931), the varieties have 90, 91, and 92 somatic chromosomes; and in other groups, the varieties show similar variation in chromosome number.

The origin of such variation is difficult to determine; although it is possible that the qualitative

changes in the chromosomes, which are presumably responsible for the specific variations, have continued to function in a larger degree within certain forms. Physiological factors may also have influenced the presence of such variation.

The frequency of polyploidy as a normal condition in somatic tissue is unknown (Gates, 1924). This increase in chromosome number in the root tips of species of the genera studied occurred only twice. In Operculina dissecta, this condition involved apparently only one tetraploid cell; while in Quamoclit lobata (Fig. 30), a similar increase in chromosome number included a large area of the root tip. The cause for such irregularities in chromosome number in Operculina dissecta and Quamoclit lobata cannot be stated; but similar conditions in other genera have been introduced experimentally by many agencies, such as certain chemicals, temperature changes, X-radiation, wounding, and insect attacks, which alter the normal processes of mitosis and cell division, or both (Gates, 1924) (Hurst, 1932). A relation of such heteroploid area or single cells to high chromosome numbers in Ipomoea and related genera is possible because of the presence in some species of vegetative reproduction by means of tuberous roots.

Hybridization

The problem of hybridization has been approached cytologically through a study of chromosome numbers and behavior, and through the resulting factors, fertility and sterility, by which these chromosome characteristics are manifested. In hybrids, all degrees of sterility and fertility are possible; and, in most cases, may be traced to the possibility or impossibility of the chromosome sets and their genes working together (Hurst, 1932).

The relation of taxonomy to hybridization and the importance of chromosome numbers in this respect (Winge, 1925) have shown that compatibility in hybridization may be conditioned by these factors; and that, in general, fertility in the hybrid decreases as the relation between the parents become more distant. In many genera, such as Anthurium (Gaiser, 1927) and Viola(Bamford & Gershoy,1930) it is apparent that crosses between species with the same chromosome number are usually more compatible than crosses involving different chromosome numbers.

Occasionally, however, the relation of compatibility in hybridization to chromosome number must be considered qualitatively, rather than quantitatively. In Ipomoea,

Quamoclit, and Calonyction all of the crosses involving similar chromosome numbers, except one, were unsuccessful; while in Phlox (Flory, 1931) a similar condition was present among varieties having the same chromosome number.

It seems probable, therefore, that in some genera there are factors other than chromosome numbers which may influence the degree of compatibility between two forms, however closely related they appear to be.

The limited success of hybridization in Ipomoea and Quamoclit indicates, nevertheless, that apparently even within these latter genera, the relationship between certain forms is more close than between others.

A cross between Quamoclit pinnata (pennata) (2n-30) (Figs. 20,22,31) and Q. coccinea (angulata) (2n-28) (Figs. 21,33) resulted in a completely sterile hybrid with 29 somatic chromosomes (Figs. 23,32). The external characters of this hybrid were about intermediate between those of the parents, and were similar to those of Quamoclit Sloteri (2n-58)(Figs.25,36). The flower of the hybrid, however, was more star shaped, and the leaf less broad and of more delicate structure than those of the latter form. A similar cross has been made in Japan (Nohara, 1930) (Kagawa & Nakajima, 1933) with identical results. Quamoclit Sloteri is a known hybrid, completely

fertile, originating from a cross between Q. Quamoclit (pinnata) and Q. coccinea made by Mr. Vincent Sloter of Vincent, Ohio, about 1912. The relation of such a form as Q. Sloteri to the hybrid in question has been suggested (Kagawa & Nakajima, 1933) through the possibility of a doubling of the chromosomes (amphidiploidy) in the second generation of a Q. Quamoclit X Q. coccinea cross, thus producing a fertile form different in its characters from the first generation. Evidence of this fertility is seen in the pollen of Q. Sloteri (Fig. 42). The lack of compatibility between Q. Sloteri and Q. coccinea is evident in the production of a completely sterile hybrid from a cross between them (Nohara, 1930). This cross was unsuccessful in the present work.

Another combination in the genus Quamoclit involving different chromosome numbers was between Q. coccinea hederifolia (2n-28) and Q. pennata (pinnata) (2n-30) (Kagawa & Nakajima, 1933). These crosses also resulted in completely sterile hybrids with 29 somatic chromosomes, and whose external characters were intermediate between those of the parents.

The only successful crosses between forms with similar chromosome numbers were between Q. coccinea hederifolia (2n-28) (Figs. 24,35) and Q. coccinea (2n-28)

(Figs. 21,33) (reciprocal). The hybrids from these crosses had the same number of chromosomes as and were about intermediate in external characteristics between the respective parents (Figs. 15, 17, 34). Both hybrids were fertile. A cross between the varieties Q. pinnata (white) (2n-30) and Q. pinnata (red)(2n-30) (Nohara, 1930) was similar in its results to that between Q. coccinea hederifolia and Q. coccinea. It is remembered that crosses in Ipomoea involving the same chromosome numbers were unsuccessful.

The appearance of a haploid plant has resulted from a varietal cross in Pharbitis nil (Ipomoea nil) between Normal and "Pine Inconstant" (U, 1930). This plant was considerably reduced in all of its parts, with various morphological characteristics. Great size variability and a high percentage of abortion of the pollen grains, as a result of irregular meiosis, was accompanied by complete sterility. The haploid condition has apparently arisen through apomicitic development of an egg.

The extensive hybridization in Russia (Tioutine, 1935) between varieties of I. batatas has led to similar investigations with other species of the genus. Crosses have been made between I. batatas and other tuberous species, I. fastigiata (I. tiliacea), I. pandurata, and

I. macrorhiza. Although this work has just begun, the best success (4%) has been received from the I. batatas X I. fastigiata combination. These hybridization studies are being carried on without knowledge of the chromosome numbers of the species involved, and it is apparent that these would be of decided value in such work. It is of interest to note that I. lacunosa, I. ramoni, and I. batatas, whose somatic chromosome numbers respectively form the series 30, 60, and 90, are in the same subsection of the genus.

A relation between chromosome number and sex is present in several genera. In Nicotiana (McCray, 1932), Viola (Bamford & Gershoy, 1930), Gossypium (Feng, 1935), and others, hybridization between forms with different chromosome numbers is more successful when the species with the higher number is the female parent. The hybrids in Quamoclit arose from female parents whose chromosome numbers were both higher and lower than the male parent; so that there appeared to be no sex influence present. This, however, may indicate that such a sex-chromosome number relatipnship exists only when the difference between the chromosome numbers of the parents is rather large.

Variation of chromosome number in many genera is, in general, accompanied by variation in chromosome size and

cell size, or both. In Carex (Heilborn, 1924), Viola (Bamford & Gershoy, 1930), and the Cactaceae (Stockwell, 1935), as a rule, the chromosome size decreases as the number increases; while in Draba(Heilborn, 1927) and Rosa (Erlanson, 1929), an increase in chromosome number is attended by an increase in cell size. The largest Draba species have the highest chromosome number, and the smallest species have the lowest chromosome number. In the Magnoliales (Whitaker, 1933) and in Linum (Martzenitzina, 1927), the species may be grouped according to the chromosome number and size; for, as a rule, the chromosomes in the higher numbers are smaller than those in the lower. Linum has five such groups; the Magnoliales have two. In some genera, such as Galeopsis (Muntzing,1927) and Anthurium (Gaiser, 1927), there is little or no relation among chromosome size, cell size, and chromosome number.

A somewhat similar condition seems to be present in Ipomoea. The chromosomes in the lower numbers are, in general, larger than those in the higher; but there appears to be no relation between variation in chromosome number and variation in cell size.

Pollen

An irregularity in size of pollen grains is, in general, present in most hybrids, such as Quamoclit

pinnata (white) X Q. coccinea, although the pollen of each parent may be of similar size.

Hybridization results in the combining of two sets of chromosomes which may, or may not, be similar; and studies in Crataegus (Longley, 1923,1924a), Rubus (Longley, 1923, 1924b), Viola (Bamford & Gershoy, 1930), and Solanum (Longley & Clark, 1930), and many other genera show that diversity in pollen grain size or complete failure in pollen formation are a direct result of irregularities in the processes of meiosis, which are conditioned by the behavior of the two sets of chromosomes.

The failure of germination of pollen in artificial media is not uncommon. The extensive investigations which have been conducted in this respect (Sandsten, 1909) (Knowlton, 1922) (Brink, 1924a,1924b,1924c,1924d) have shown that, in general, pollen of species, and even of members within a species, vary in their growth requirements. In Viola (Gershoy, 1934), the pollen of species in one section will not germinate in a medium which is suitable for pollen growth of species in other sections.

Summary

1. The chromosome numbers of sixty-four species, varieties, and hybrids of Ipomoea, Quamoclit, Calonyction, Operculina, and Merremia are presented.

2. Thirty-seven species and varieties of Ipomoea have the constant number of 30 somatic chromosomes.

3. Divergence from the homoploid series in Ipomoea is found in the 60 somatic chromosomes of I. ramoni and the 90 somatic chromosomes of ten varieties of I. batatas.

4. It is suggested that I. ramoni and I. batatas are related to the other species of the genus through hybridization, followed by chromosome doubling.

5. The investigated species of Calonyction, Operculina, and Merremia each have 30 chromosomes; while in Quamoclit, three species have 28, three varieties of one species have 30, and one species has 58 somatic chromosomes.

6. Chromosome doubling was found in Operculina dissecta and Quamoclit lobata. The cause of this doubling cannot be stated.

7. Interspecific and intergeneric hybridization was attempted. All crosses involving similar chromosome numbers, except one, were unsuccessful. The three recognized hybrids produced were from crosses within the genus Quamoclit. The cross Q. coccinea hederifolia (2n-28) X Q. coccinea (2n-28) (reciprocal) resulted in fertile hybrids with 28 somatic

chromosomes, and whose external characters were about intermediate between the parents. The cross Q. pinnata (white) (2n-30) X Q. coccinea (2n-28) resulted in a sterile hybrid with 29 somatic chromosomes, and whose external characteristics were also about intermediate between the parents, and which somewhat resembled Q. Sloteri (2n-58).

8. There was, in general, a decrease in chromosome size with an increase in chromosome number, but no relation seemed to exist between variation in chromosome number and variation in cell size.

9. Pollen of the hybrid, Q. pinnata (white) X Q. coccinea, varied in size, although that of each parent was of similar size. Pollen germination on artificial media was unsuccessful.

The writer wishes to express his appreciation to Dr. Ronald Bamford, who suggested the problem; and under whose direction, the work has been carried on.

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EXPLANATION OF PLATES

All of the figures of plates I to V inclusive (Figures 1-25) were drawn with the aid of a camera lucida, a Zeiss 90X apochromatic objective, and a 15X compensating ocular. The approximate magnification is 2750.

The approximate magnifications for the photomicrographs on Plates VI, IX, X and XI are given for each figure separately.

PLATE I

Figure 1. *Ipomoea digitata*. Chromosome plate of a P.M.C. in the first division metaphase. n-15.

Figure 2. *Ipomoea digitata*. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 3. *Ipomoea pandurata*. Somatic chromosome plate fro a root tip cell. 2n-30

Figure 4. *Ipomoea pandurata*. Chromosome plate of a P.M.C. in the second division metaphase. n-15.

Figure 5. *Ipomoea ramoni*. Somatic chromosome plate from a root tip cell. 2n-60.

PLATE 1

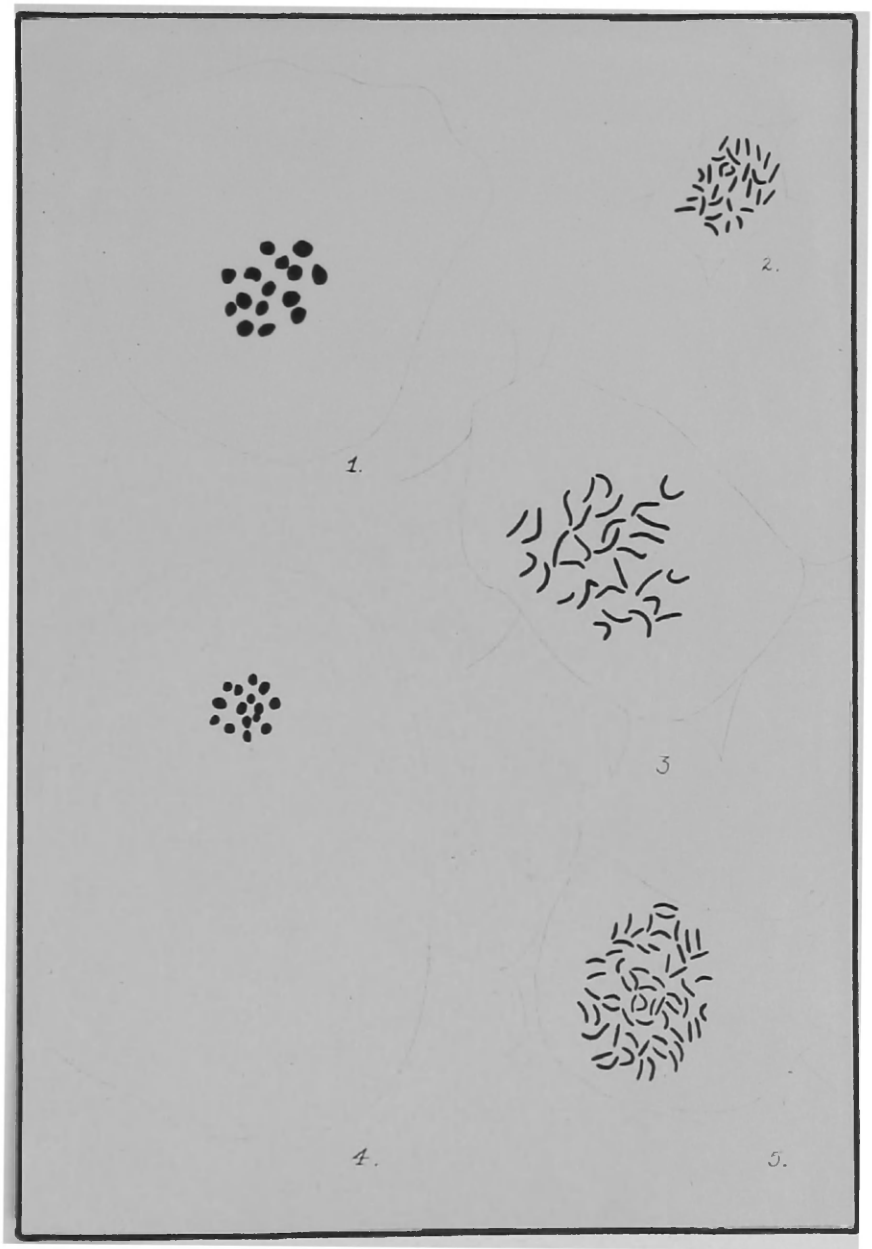

PLATE II

Figure 6. Calonyction aculeatum var. Christmas Vine. Chromosome plate of a P.M.C. in the first division metaphase. n-15.

Figure 7. Calonyction aculeatum var. Christmas Vine. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 8. Calonyction aculeatum. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 9. Calonyction aculeatum. Chromosome plate of a P.M.C. in the second division metaphase. n-15.

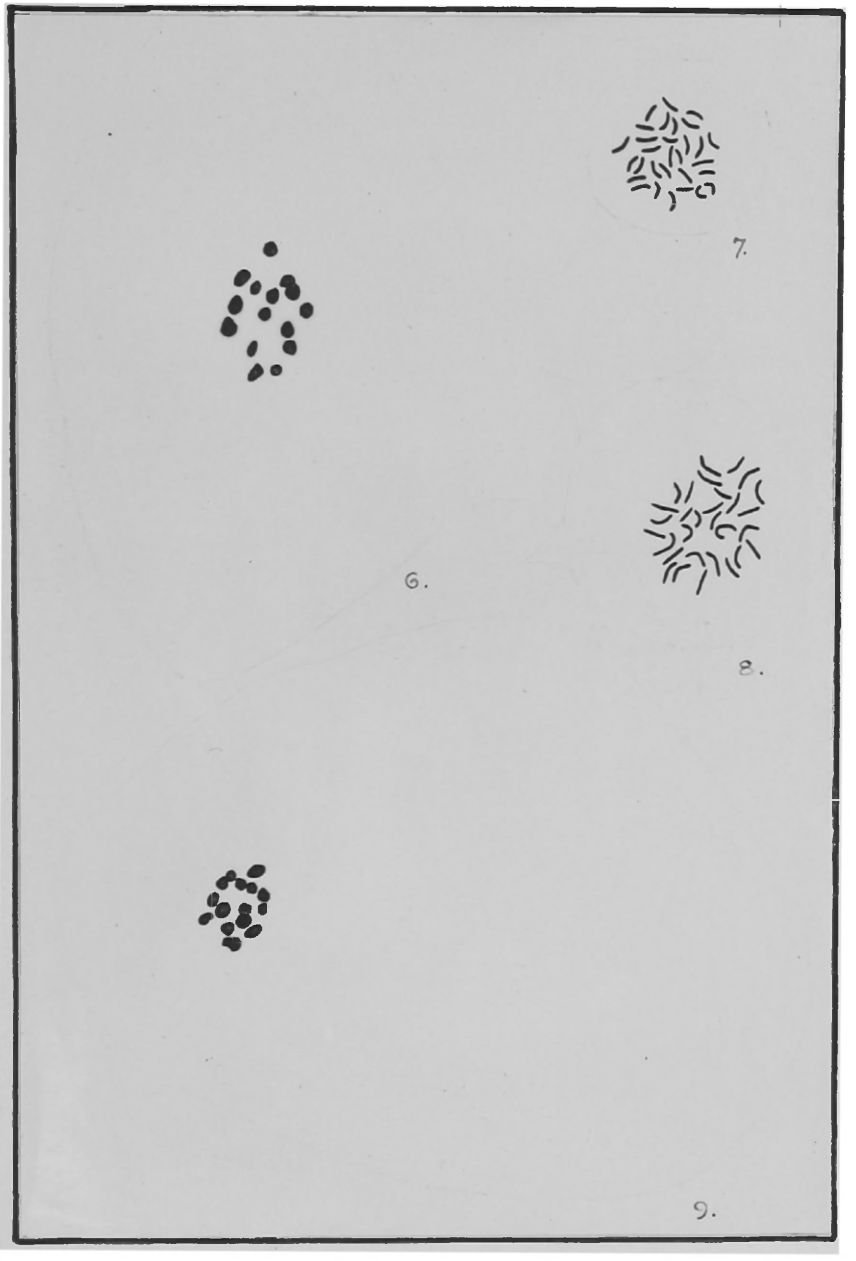
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PLATE III

Figure 10. *Ipomoea batatas* var. Vineland Bush. Somatic chromosome plate from a root tip cell. 2n-90.

Figure 11. *Ipomoea lacunosa*. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 12. *Ipomoea purpurea* var. Double Semi-double. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 13. *Ipomoea purpurea*. var. Double Semi-double. Chromosome plate of a P.M.C. in the second division metaphase. n-15.

Figure 14. *Ipomoea arborescens*. Somatic chromosome plate from a root tip cell. 2n-30.


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PLATE IV

Figure 15. Hybrid. *Quamoclit coccinea hederifolia* X *Q. coccinea*. Chromosome plate of a P.M.C. in the first division metaphase. n-14.

Figure 16. *Ipomoea setosa*. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 17. Hybrid. *Quamoclit coccinea hederifolia* X *Q. coccinea*. Somatic chromosome plate from a root tip cell. 2n-28.

Figure 18. *Operculina tuberosa*. Somatic chromosome plate from a root tip cell. 2n-30.

Figure 19. *Ipomoea setosa*. Chromosome plate of a P.M.C. in the first division metaphase. n-15.

PLATE IV

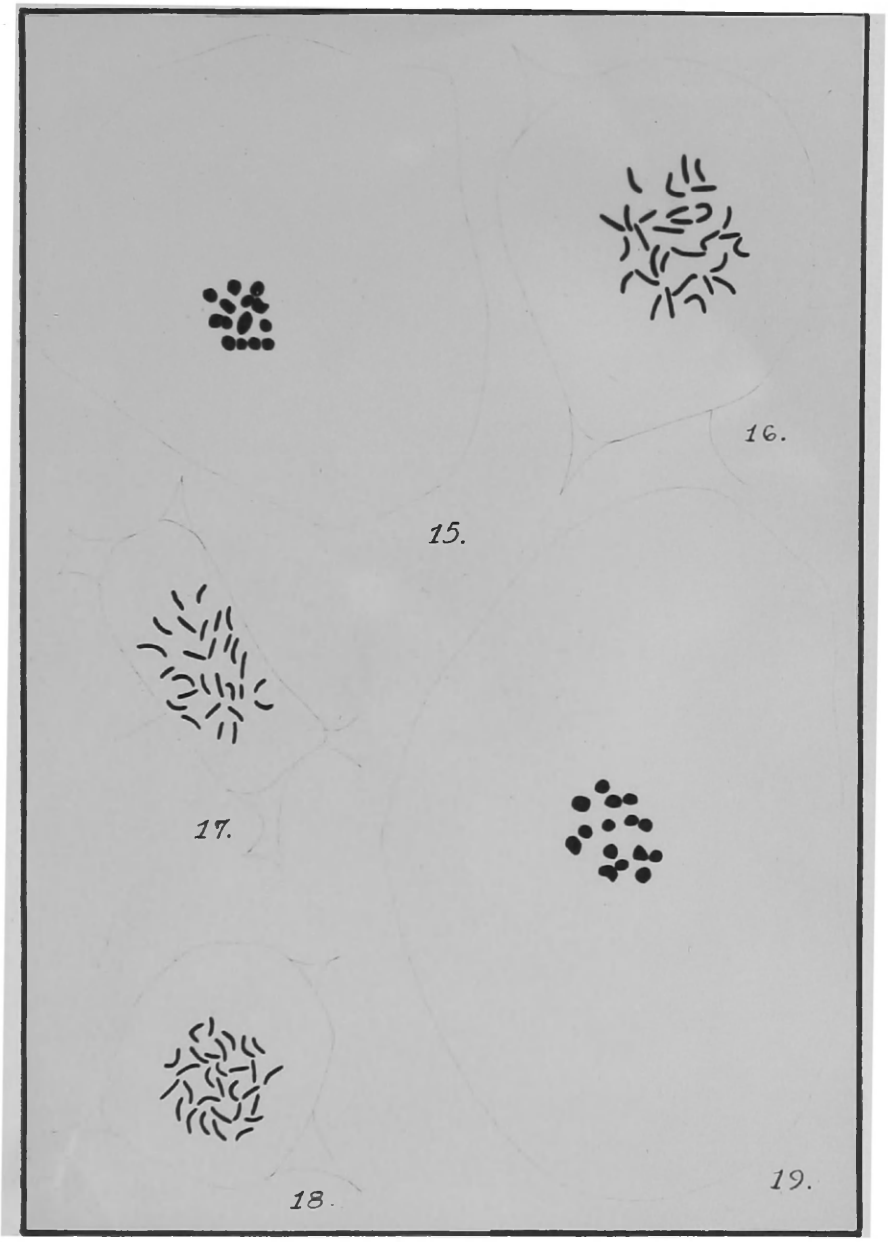

PLATE V

Figure 20. Quamoclit pinnata (white). Chromosome plate of a P.M.C. in the first division metaphase. n-15.

Figure 21. Quamoclit coccinea. Somatic chromosome plate from a root tip cell. 2n-28.

Figure 22. Quamoclit pinnata (white). Somatic chromosome plate from a root tip cell. 2n-30.

Figure 23. Hybrid. Quamoclit pinnata (white) X Q. coccinea. Somatic chromosome plate from a root tip cell. 2n-29.

Figure 24. Quamoclit coccinea hederifolia. Somatic chromosome plate from a root tip cell. 2n-28

Figure 25. Quamoclit Sloteri. Somatic chromosome plate from a root tip cell. 2n-58.

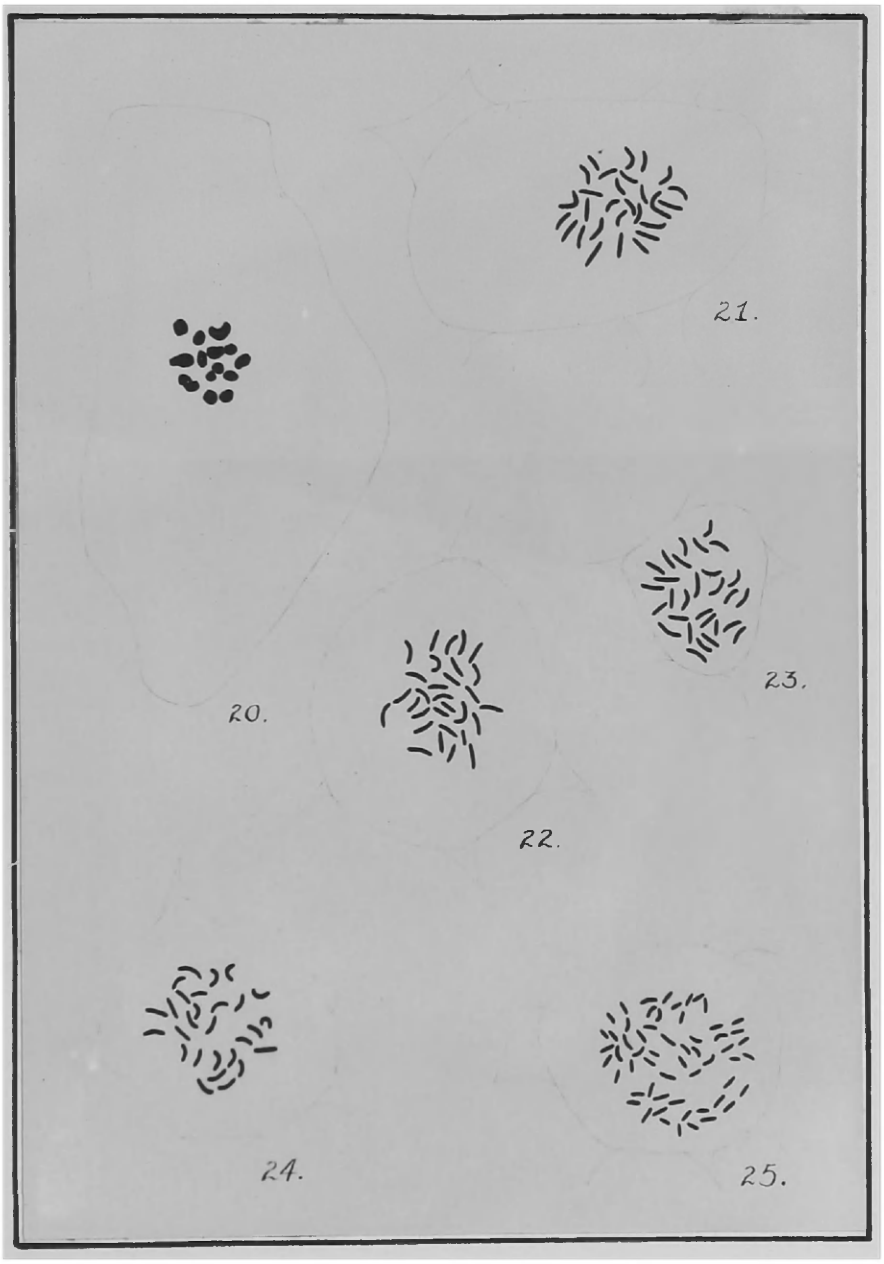
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PLATE VI

Figure 26. *I. cairica*. Photomicrograph of a somatic chromosome plate from a root tip cell. 2n-30. 1650X

Figure 27. Photomicrograph of a chromosome plate of the second division metaphase, showing good fixation of this stage of meiosis. 1650X

Figure 28. Photomicrograph of diakineses in a pollen mother cell, showing good fixation in this stage of meiosis. 650X

Figure 29. *I. ramoni*. Photomicrograph of a somatic chromosome plate from a root tip cell, showing the polyploid chromosome number (amphidiploidy). 2n-60. 1300X

Figure 30. *Q. lobata*. Photomicrograph of a somatic chromosome plate from a root tip, showing tetraploid cells in the diploid root. 1650X

PLATE VI

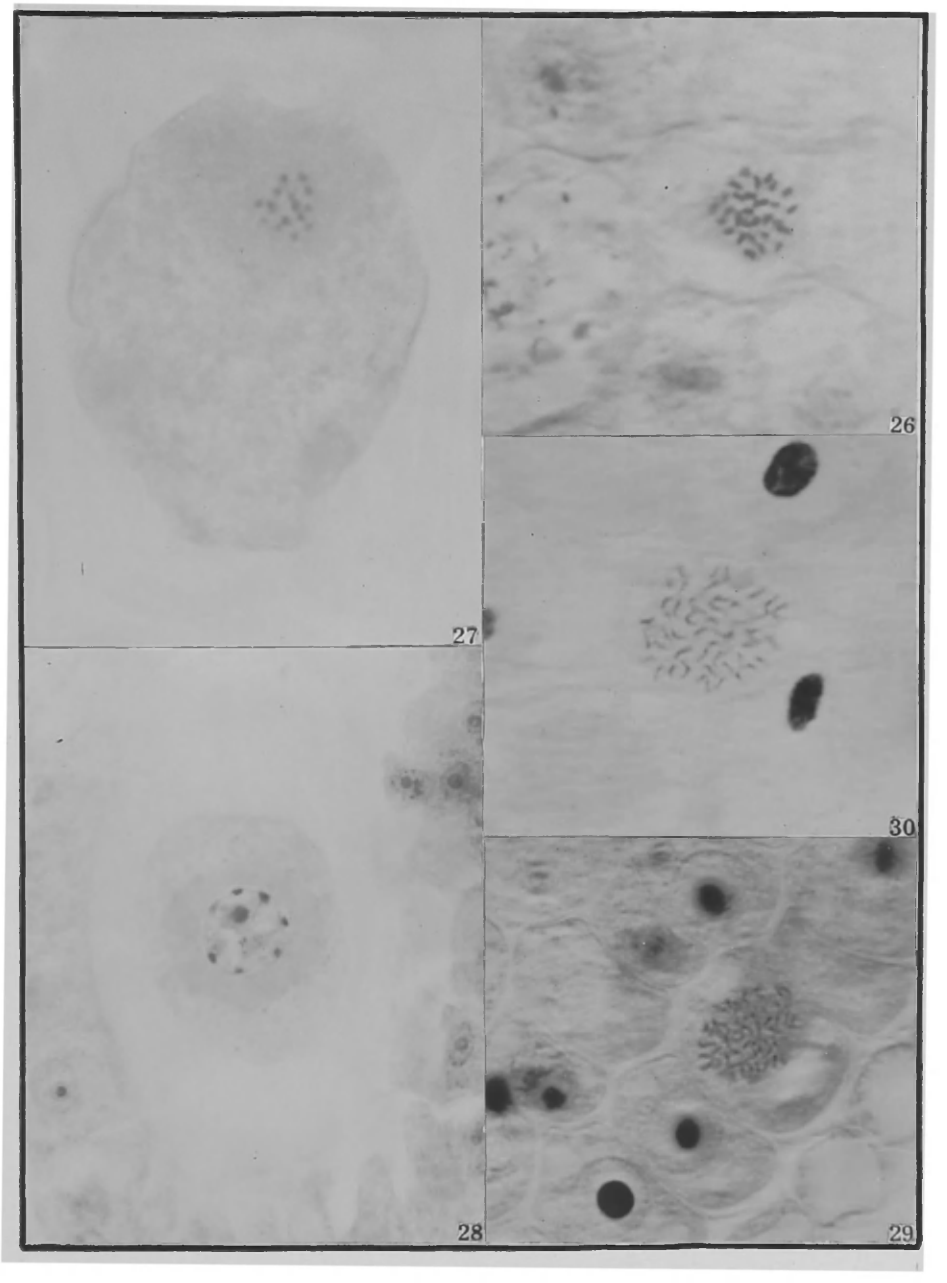

PLATE VII

Figure 31. *Quamoclit pinnata* (white.)

Figure 32. Hybrid, *Quamoclit pinnata* (white) X *Q. coccinea.*

Figure 33. *Quamoclit coccinea.*

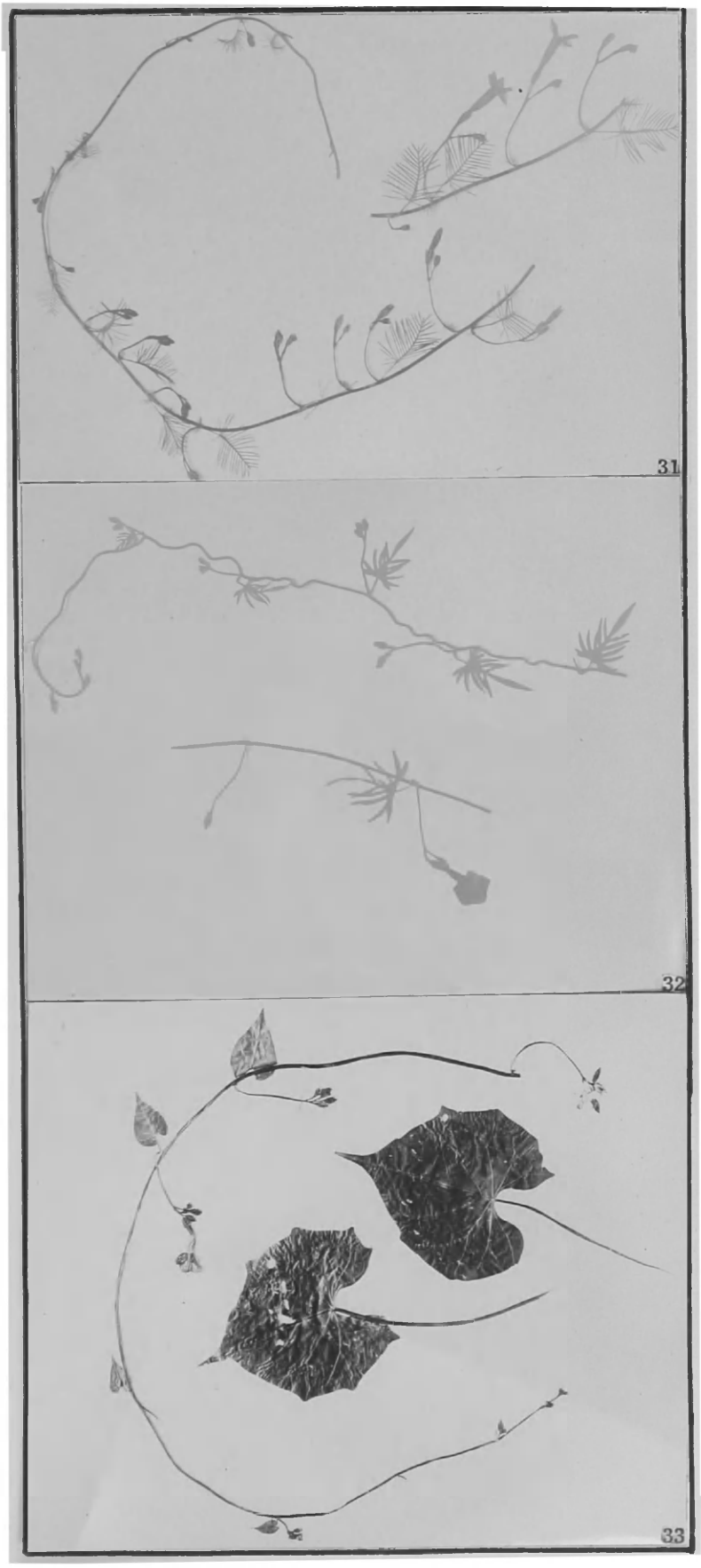
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PLATE VIII

Figure 34. Hybrid, *Quamoclit coccinea* X *Q. coccinea hederifolia*.

Figure 35. *Quamoclit coccinea hederifolia*.

Figure 36. *Quamoclit Sloteri*.

PLATE VIII

PLATE IX

Figure 37. Photomicrograph of the pollen of Quamoclit pinnata (white). 100X

Figure 38. Photomicrograph of the pollen of the hybrid, Quamoclit pinnata (white) X Q. coccinea. 100X

Figure 39. Photomicrograph of the pollen of Quamoclit coccinea. 100 X

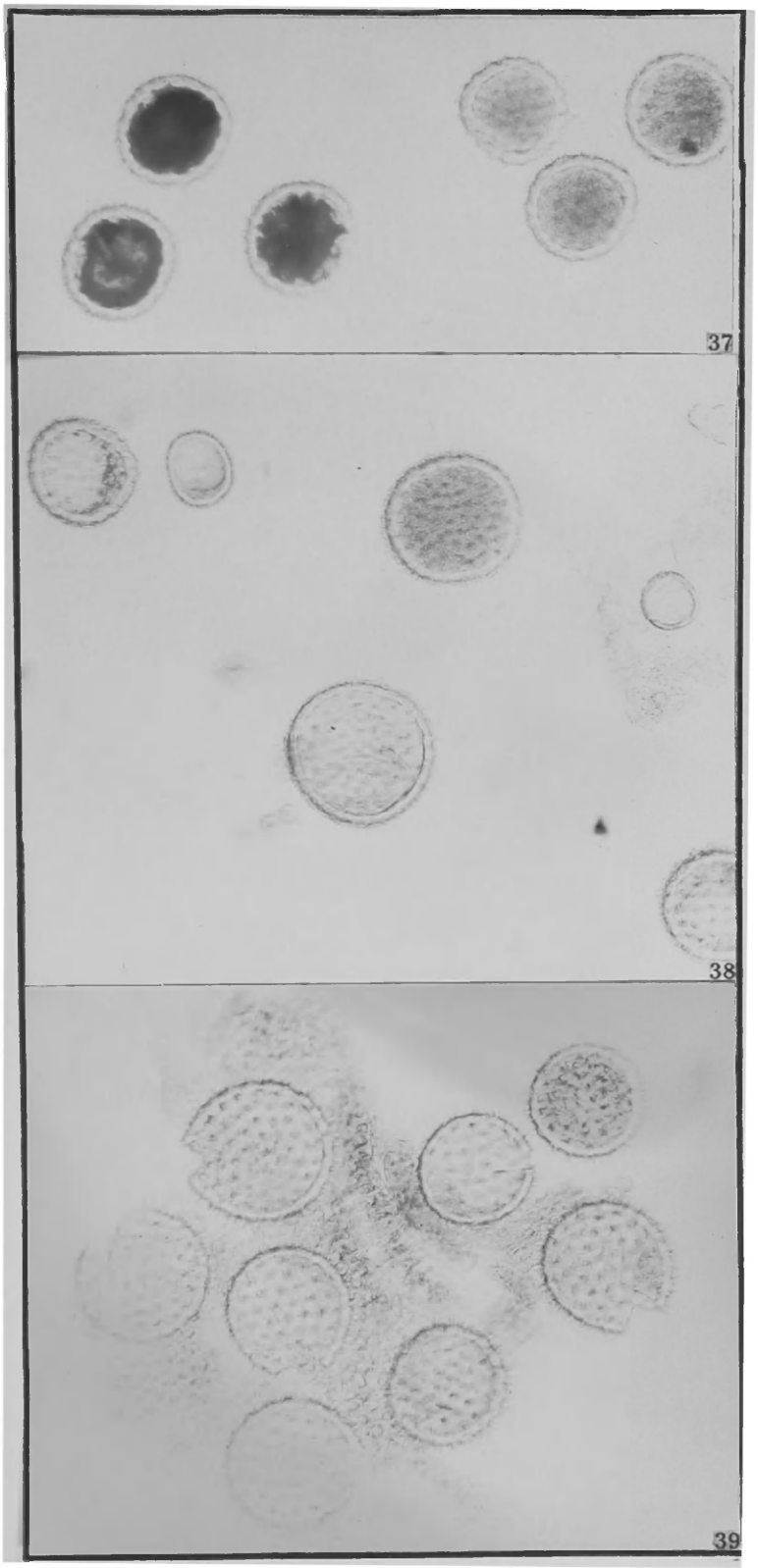
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PLATE X

Figure 40. Photomicrograph of the pollen of the hybrid, Quamoclit coccinea hederifolia X Q. coccinea. 100X

Figure 41. Photomicrograph of the pollen of Quamoclit coccinea hederifolia. 100X

Figure 42. Photomicrograph of the pollen of Quamoclit Sloteri. 100X

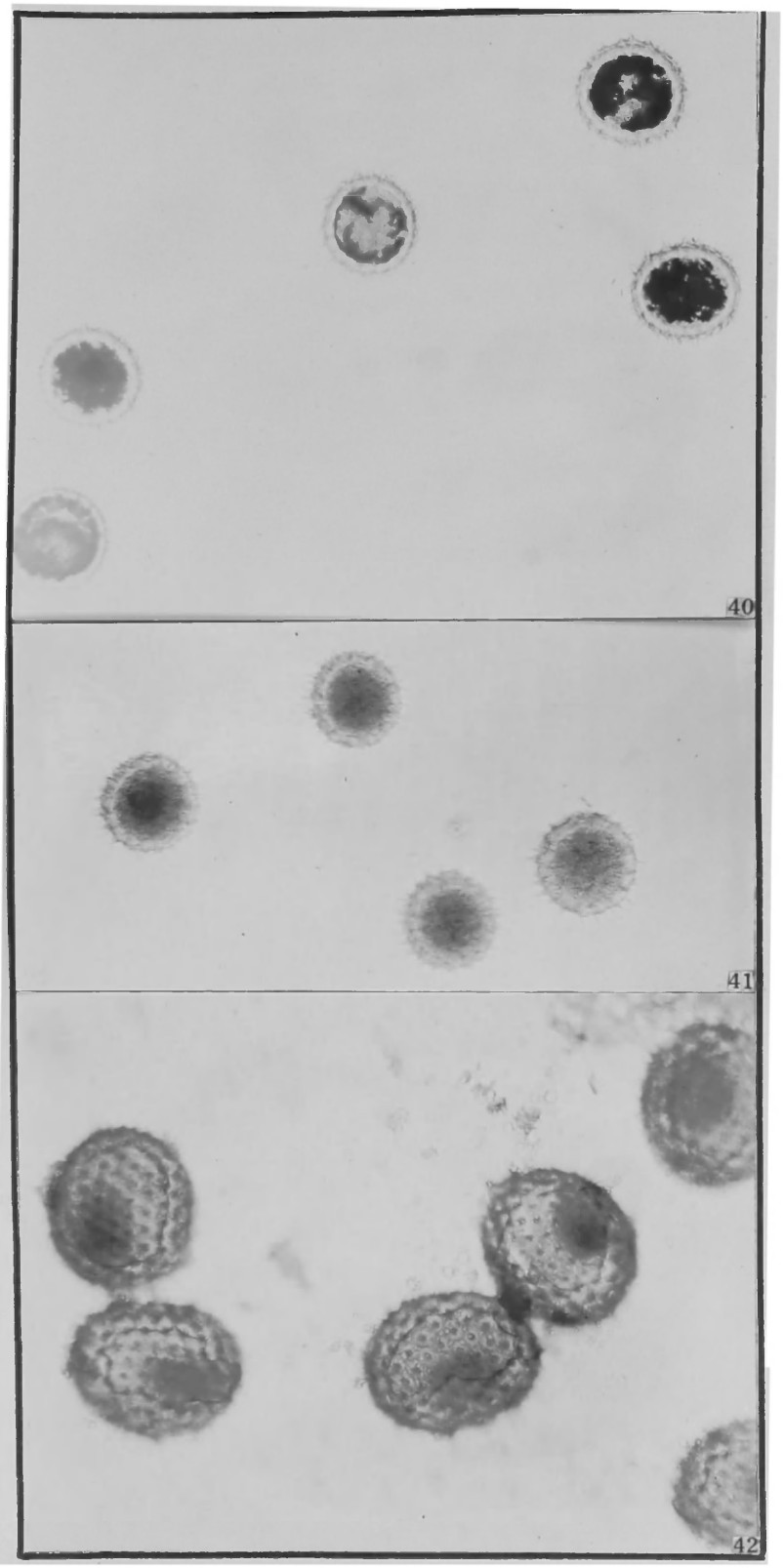
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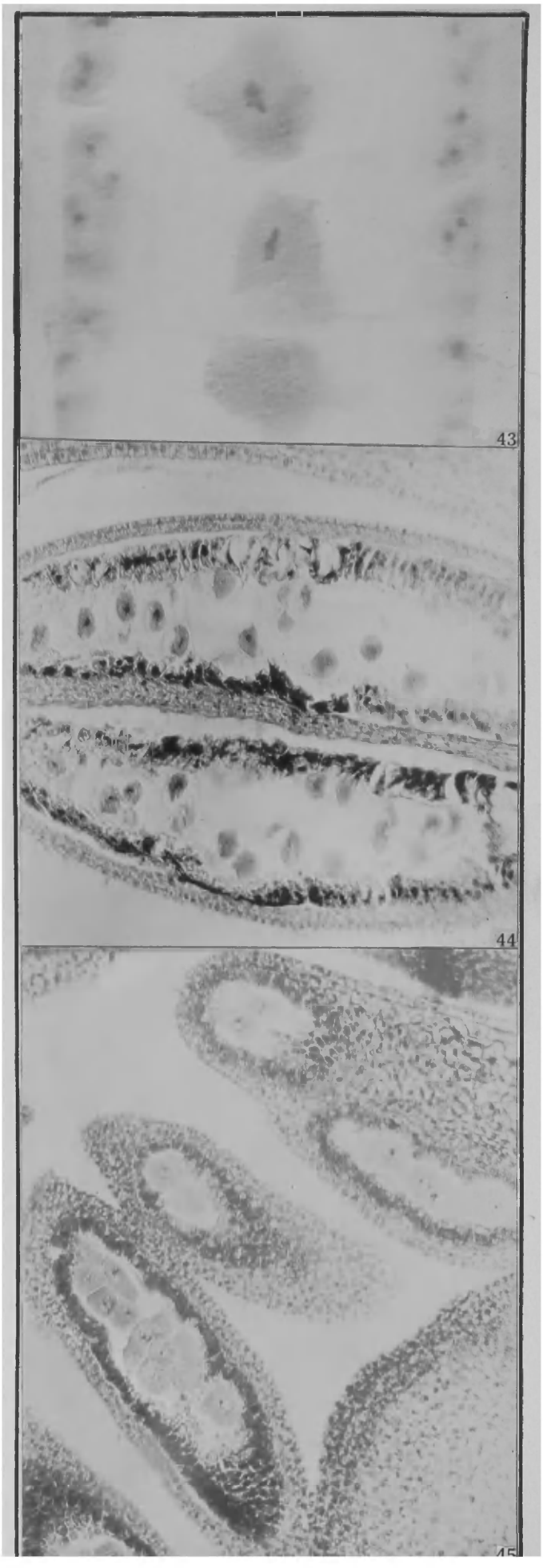
PLATE XI

Figure 43. Photomicrograph of pollen mother cells in the first division, showing clumping of the chromosomes, as a result of poor fixation. 700X.

Figure 44. Photomicrograph of pollen mother cells in the first division. This shows the results of poor fixation in the whole anther. 175X.

Figure 45. Photomicrograph of anthers, showing good fixation of pollen mother cells in the prophase stages of meiosis. 175X.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