Chromosome Numbers of Some Species of *Passiflora* Occurring in Hawaii[1]

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INTRODUCTION

PASSIFLORA IS A GENUS of approximately 400 species of plants, mostly woody or herbaceous vines. About 360 species are native to tropical and subtropical North and South America and adjacent islands. The remainder are indigenous to southeastern Asia, a number of south Pacific islands, and Madagascar (Killip, 1938: 9). Man has been instrumental in disseminating many of the species with edible fruits or with highly colored, attractive flowers, and representatives of the genus are now to be found in most tropical lands throughout the world.

Several species of *Passiflora* have been introduced into the Hawaiian Islands for cultivation for their edible fruits (Pope, 1935). Additional species have been introduced for growing as garden ornamentals. A number of species, both edible and ornamental, have escaped from cultivation and are now to be found in a naturalized wild state along waysides, on waste lands, and in lower forest regions (Pope, 1929: 149). A total of 22 species has recently been reported as occurring in Hawaii (Neal, 1948: 522–525).

A number of edible species, of which *P. edulis* is the most important, are cultivated as commercial crops in Australia, New Zealand, and South Africa, where extensive use is made of the fruit. Their culture is practiced to a lesser degree in various other tropical countries, and in Florida, California, and Hawaii. Numerous ornamental species and species-hybrids constitute an important item in the plant nursery business in the United States and elsewhere.

Nurserymen have enjoyed some success in producing interspecific hybrid varieties for the floricultural trade. Fruit breeders, on the other hand, have had little or no success in attempts to improve upon existing edible types through interspecific hybridization, largely because of hybrid sterility.

Cytological studies of plants often serve as a useful adjunct to plant breeding problems. Chromosome numbers and chromosome behavior frequently indicate origins of species and relationships between species, and provide clues as to which species are most likely to be compatible upon crossing. Despite the amount of breeding which has been done among species of *Passiflora,* in Hawaii and elsewhere, the genus is but poorly understood from the standpoint of cytology. The recently published *Chromosome Atlas of Cultivated Plants* lists the chromosome numbers of only seven species (Darlington and Janaki Ammal, 1945: 114).

This paper deals principally with reporting the chromosome numbers of additional species of *Passiflora* as well as of a number of botanical varieties and forms, interspecific hybrids, and an intraspecific chromosomal race. Notes on cytological behavior have been added where they might be helpful in clarifying origins or relationships.

MATERIALS AND METHODS

Chromosome numbers were determined for all species of *Passiflora* of which material for study could be obtained in Hawaii. Counts were made from root tips of seedling plants

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or rooted cuttings, and, whenever possible, from suitable flowering material. Root tips were stained by the crystal-violet–iodine method following Randolph's (1935) schedule. Anthers from young buds were examined in smear preparations with the use of iron-acetocarmine (Belling, 1926).

The figures were drawn with the aid of a camera lucida.

OBSERVATIONS

All species and subspecific forms for which chromosome numbers have been determined are listed in Table 1. They are placed in the table in the order in which they occur in Killip's (1938) systematic treatment of the genus. Interspecific hybrids which are not included in Killip's treatment are placed at the bottom of the table. The list comprises 16 species, 1 botanical variety, 4 botanical forms, 4 interspecific hybrids, and a polyploidal race of one species.

Six of the seven species listed in the chromosome atlas of cultivated plants (Darlington and Janaki Ammal, 1945: 114) are reported to occur in Hawaii (Neal, 1948: 522–525). These species are *P. caerulea* L., *P. edulis* Sims., *P. foetida* L., *P. incarnata* L., *P. quadrangularis* L., and *P. racemosa* Brot., all of which are reported to have chromosome numbers of 2n = 18. The seventh species, *P. lutea* L., with a chromosome number given as "2n = 84?," is not known to be in the islands. Of the 22 species listed by Neal (loc. cit.), the writer was unable to obtain material of the following seven: *P. alata* Dry., *P. coccinea* Aubl., *P. antioquiensis* Karst., *P. kermesina* Link and Otto, *P. racemosa* Brot., *P. Banksii* Benth., *P. fruticosa* Killip.

TABLE 1

CHROMOSOME NUMBERS OF VARIOUS SPECIES, SUBSPECIFIC FORMS, AND INTERSPECIFIC HYBRIDS OF *Passiflora*

PASSIFLORA SPECIES	CHROMOSOME NUMBER	
	N	2N
P. suberosa L.	12	24
P. suberosa (triploid)	18*	36
P. lutea L.	----	84?†
P. pulchella HBK	6	12
P. mollissima (HBK) Bailey	----	18
P. manicata (Juss.) Pers.	----	18
P. vitifolia HBK	9	18
P. quadrangularis L.	----	18
P. ligularis Juss.	----	18
P. Seemanni Griseb.	9	18
P. maliformis L.	9	18
P. laurifolia L.	9	18
P. incarnata L.	----	18
P. edulis Sims	9	18
P. edulis form *flavicarpa* Degener	9	18
P. caerulea L.	9†	18†
P. subpeltata Ortega	9	18
P. foetida L.	10	20‡
P. foetida (3 variant forms)§	10	20
P. foetida variety *gossypifolia* (Desv.) Mast.	10	20
P. Pfordti (= *alata* Dry. × *caerulea* L.)	----	18
P. maliformis L. × *laurifolia* L.	----	18
×*P. caerulea* L. (hybrid) (Degener, 1934)	----	18
P. princeps-coccinea (= *racemosa* Brot. × *coccinea* Aubl.)	9†	18†

* Some meiotic irregularity.
† Reported in *Chromosome Atlas* (Darlington and Janaki Ammal, 1945: 114); not seen by author.
‡ Reported as 2n = 18 by Janaki Ammal (Darlington and Janaki Ammal, 1945: 114).
§ Variety or form names, if any, not determined by writer.

On the basis of somatic chromosome numbers which are reported in Table 1 and of numbers previously reported in the literature, all of the species, hybrids, and varieties investigated to date may be classified into six chromosome number groups. These groups and the species belonging to them are as follows:

2n = 12—*P. pulchella*

2n = 18—*P. mollissima; P. manicata; P. vitifolia; P. quadrangularis; P. ligularis; P. Seemanni; P. maliformis; P. laurifolia; P. maliformis* × *laurifolia; P. racemosa; P. coccinea; P. racemosa* × *coccinea; P. incarnata; P. edulis; P. edulis* f. *flavicarpa; P. alata; P. caerulea; P. alata* × *caerulea (Pfordti);* × *P. caerulea; P. subpeltata; (P. foetida ?).*

2n = 20—*P. foetida,* and 3 variant forms; *P. foetida* var. *gossypifolia.*

2n = 24—*P. suberosa*

2n = 36—*P. suberosa*

2n = 84?—*P. lutea*

The 2n = 12 group consists of but a single species, *P. pulchella.*

The 2n = 18 group comprises 15 species, 4 interspecific hybrids, and 1 botanical form, with 1 species doubtful. Janaki Ammal (loc. cit.) determined the somatic chromosome number of *P. foetida* to be 18. The writer, on the other hand, has examined considerable material of *P. foetida,* its botanical variety *gossypifolia,* and several variations, all of which occur as common wayside weeds in Hawaii, and has never failed to find 20 somatic chromosomes (Fig. 1). Examinations of dividing sporocytes have consistently revealed 10 bivalents normally paired (Fig. 2). The writer, therefore, is disposed to place *P. foetida* in a separate group consisting only of itself and its varieties. The possibility is not excluded, however, that the Hawaiian representatives of the species may be aberrant forms. *P. foetida* probably was limited to a single introduction from which all of the plants presently populating the several islands are derived.

FIG. 1. Mitotic metaphase in *P. foetida* root tip showing 20 somatic chromosomes.

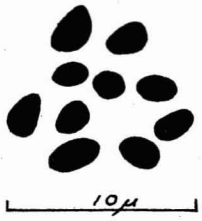

FIG. 2. Meiotic metaphase I in *P. foetida* showing 10 bivalent chromosomes.

Microsporogenesis was observed to proceed along a normal course in all of the species in the 2n = 18 group. A single exception was noted in *P. subpeltata,* in which syndiploidy occurred in one locule of an anther. The sporocytes in this locule were seen at diakinesis to have 2 large nucleoli and 18 pairs of associated chromosomes instead of the usual 9 pairs. There seemed to be no strong tendency to form multivalent configurations, and it is supposed that such sporocytes would have proceeded to give rise to diploid microspores. The condition very probably arose through failure of a mitotic anaphase in the meristem from which the sporogenous tissue was derived.

Pope (1935: 11) proposed a hybrid origin for *P. edulis* f. *flavicarpa,* possibly as a cross between *P. edulis* and *P. ligularis.* The supposition is not borne out in studies of cytological behavior, for meiosis is normal in every respect (Fig. 3), and both the ovules and the pollen grains are fully viable. The

chromosome number of 18 shows that the plant is not a double diploid, and, therefore, in view of its full fertility, very probably not an interspecific hybrid. A review of the history of *flavicarpa* points to a more probable origin as a mutation of *P. edulis.* There are several notable differences between typical *edulis* and form *flavicarpa,* however, including a high degree of cross incompatibility. The two forms of the species deserve more study from the standpoints of both cytology and genetics.

FIG. 3. Meiotic metaphase I in *P. edulis* form *flavicarpa* showing 9 bivalent chromosomes.

No flowering material of *P. Pfordti, P. maliformis* × *laurifolia,* × *P. caerulea,* or *P. princeps-coccinea* could be obtained by the writer for studies of chromosome behavior at meiosis in these interspecific hybrids. All four appear to be completely sterile.

P. suberosa is the sole representative of the 2n = 24 group. Microsporogenesis is normal in the species, but there is evidence of strong secondary association between the bivalents at the first metaphase (Fig. 4). Secondary association in meiosis has been regarded as indicative of an earlier polyploidal origin (Darlington 1932: 219–223).

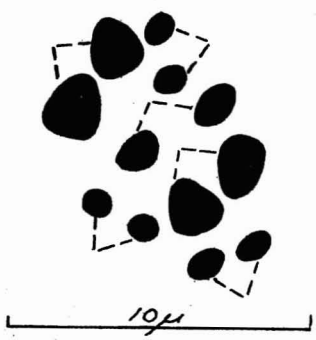

FIG. 4. Meiotic metaphase I in *P. suberosa* showing 12 bivalent chromosomes. Broken lines indicate pairs of bivalents in secondary association.

P. suberosa is also the sole representative of the 2n = 36 group. This 36-membered form is undoubtedly an autotriploid derivative of the 24-membered form, constituting a separate chromosomal race within the species. There are no conspicuous morphological differences between the two forms. The only distinguishable differences are to be found in the slightly larger leaves and a slight intensification of anthocyanin pigmentation in the young stems and on the dorsal surfaces of the sepals of the flowers of the triploid form. The species, however, is highly polymorphic, with all degrees of intergradation among its numerous variants, so that even these differences are not entirely reliable as a means of distinguishing the two races in nature. The triploid race appeared spontaneously among wild populations of the diploid race, the first collection being made in 1937. It produces fertile seeds, and has continued to reproduce and spread under natural conditions. Examinations of all herbarium sheets of collections made prior to 1937 in the Bernice P. Bishop Museum at Honolulu reveal none which might conceivably be the triploid form.

Contrary to what might be expected of an autotriploid, triploid *P. suberosa* goes through microsporogenesis with a fairly high degree of regularity and produces a preponderance of normal quartets of microspores. Megasporogenesis must be equally little disturbed, for the fruit produces a complement of seeds more or less comparable to that produced by the diploid. Multivalent chromosome configurations were observed in a few microsporocytes, indicating that there is some disturbance to normal bivalent pairing. In an occasional sporocyte, all orders of association from univalence to sexivalence have been observed. Anaphasic separation into equal

numbers appears to be effected rather uniformly despite multivalence, however, for daughter nuclei were rarely seen to contain more than, or fewer than, 18 chromosomes. There are extremely few abnormal microspore quartets, and correspondingly few abortive pollen grains.

DISCUSSION

Darlington and Janaki Ammal (1945: 114) give $x = 9$ as the basic chromosome number of the genus *Passiflora.* This number was doubtless assumed on the basis of 6 species with $2n = 18$ and one species which was reported as "$2n = 84$?." Determination of $n = 6$ for *P. pulchella* indicates that not 9 but a lower number probably is basic in the genus. With the exception of the aberrant species *P. foetida* ($2n = 20$), all of the species examined, including *P. lutea* ($2n = 84$?), comprise a polyploid series of which the monoploid number is 6. It is recognized that the total of 29 species and variant forms for which chromosome numbers are known or presumed is but a meager sample from a genus with over 400 known species, so it seems not unreasonable to suppose that other numbers, both euploid and aneuploid, may exist among species unreported here.

It is perhaps significant from the breeders' standpoint that all of the horticultural forms studied occur in the $2n = 18$ group. These forms exhibit a fairly high degree of interspecific compatibility, as evidenced by the numerous hybrids recorded (Bailey, 1935: 2487); but the hybrids themselves are almost invariably sterile. Their compatibility suggests closeness in relationship and, possibly, a common origin.

With an assumed basic number of $x = 6$ for the genus, the species in the $2n = 18$ group must be regarded as triploids. Triploidy, however, is generally considered to be a hindrance to the origin of fertile species because of the high order of meiotic irregularity which it induces. It seems unlikely, therefore, that the majority of species examined, all of which are fertile, have originated through triploidy. An assumed basic number of $x = 3$ would afford a number of more nearly reasonable explanations of the origin of $2n = 18$ species. These species could then be regarded as hexaploids of more or less ancient origin. As has occurred in many polyploid species of plants, cytological evidence of genomic composition has disappeared in the course of speciation and stabilization except in chromosome numbers.

How speciation within a group could occur is illustrated by the mutation from *P. edulis* to the form *flavicarpa.* The nature of the mutation has not been studied, but when it occurred it must have been drastic. The form differs from the species in several foliar and stem characters. The fruit is yellow instead of purple, and the seeds are brown instead of black. In addition, the flowering habit has been modified from strictly diurnal to partly nocturnal, and a barrier of almost complete incompatibility seems to have arisen between the mutant form and the species from which it is presumed to be derived. As mentioned earlier, the hybrid origin which was suspected by Pope (1935: 11) is not borne out by cytological studies.

P. foetida ($2n = 20$) and its varieties make up a group divergent from the euploid series to which all other species examined belong. Cytological studies to date have provided no clue to its probable origin. The possibilities exist either that it arose as a secondary polyploid from a $2n = 18$ species or that it belongs to a second euploid series, perhaps with a monoploid number of 5, for which additional species have yet to be discovered. If the plants growing in Hawaii are truly representative of the species, Janaki Ammal's (loc. cit.) determination of $2n = 18$ as the chromosome number must be considered to be in error.

As noted earlier, strong secondary association in *P. suberosa* ($2n = 24$) is taken as indicative of its polyploidal origin. The 36-membered form undoubtedly originated fairly recently as an autotriploid as shown by the absence of marked morphological differences in plant characters. It is supposed that triploidy resulted in the species through the mating of an unreduced gamete with a normal, reduced gamete. How the unreduced gametes might have been produced is suggested by the case of syndiploidy observed in an anther of *P. subpeltata.*

The occasional occurrence of all degrees of multivalence up to and including sexivalence lends credence to the supposition that the $2n = 24$ form is itself polyploid, at least tetraploid if not of a higher order of polyploidy, and that the derived form is at least hexaploid. The presence of 6 genomes, although bringing about some slight degree of irregularity in meiosis, allows for more or less normal anaphasic separation into two gametic 18-chromosome complements.

CONCLUSION

The study has shown that the basic chromosome number for the genus is at most $x = 6$, and may possibly be $x = 3$, rather than $x = 9$ as indicated by Darlington and Janaki Ammal (1945: 114). It has also called attention to the discrepancy in chromosome number determinations for *P. foetida.* It is thought by the writer that the aneuploid number of *P. foetida* presages the existence of another euploid series in the genus. The determinations made bring to 29 the number of species and variant forms for which chromosome numbers are known or may be assumed from the composition of various hybrids.

It seems highly probable that there may exist chromosome numbers other than those reported here among the 300-odd species of *Passiflora* which have not been examined. Studies of a greater number of species more fully representing the recognized taxonomic groups and of additional interspecific hybrid material would aid considerably in determining origins and relationships within the genus.

REFERENCES

BAILEY, L. H. 1935. *The standard cyclopedia of horticulture.* 3 vols. xxiv + 3639 pp., 4056 figs., 120 pls. The Macmillan Company, New York.

BELLING, J. 1926. The iron-acetocarmine method of fixing and staining chromosomes. *Biol. Bul.* 50: 160–162.

DARLINGTON, C. D. 1932. *Recent advances in cytology.* xviii + 559 pp., 109 figs., 8 pls. P. Blakiston's Son and Company, Inc., Philadelphia.

——— and E. JANAKI AMMAL. 1945. *Chromosome atlas of cultivated plants.* 397 pp. George Allen and Unwin, Ltd., London.

DEGENER, O. 1932–1934. *Flora Hawaiiensis.* (Looseleaf), illus. Author, Honolulu.

KILLIP, E. P. 1938. *The American species of Passifloraceae.* Field Mus. Nat. Hist., Bot. Series 19, parts 1 and 2, publ. No. 407 and 408, 613 pp., 2 figs. Chicago.

NEAL, MARIE C. 1948. *In gardens of Hawaii.* 805 pp., 312 figs. Bernice P. Bishop Mus. Honolulu.

POPE, W. T. 1929. *Manual of wayside plants of Hawaii.* 289 pp., 160 pls. Advertiser Publishing Company, Ltd., Honolulu.

——— 1935. *The edible passion fruit in Hawaii.* Hawaii Agr. Expt. Sta., Bul. 74. 22 pp., 7 figs.

RANDOLPH, L. F. 1935. A new fixing fluid and a revised schedule for the paraffin method in cytology. *Stain Tech.* 10: 95.