

Hybridity, Polyploidy and Change in Breeding System in a *Ruellia* Hybrid

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Summary. *Ruellia tweediana* and *R. tuberosa* are large flowered chasmogamous diploids ($n = 17$) with normal meiosis and fertility. F_1 hybrids, successful in only one direction (*R. tweediana* \times *R. tuberosa*), are vegetatively vigorous and possess 17 often heteromorphic bivalents with high degree of segregational irregularities. It is exclusively cleistogamous and completely pollen and seed sterile. Like F_1 , the artificial amphidiploid ($n = 34$) is also cleistogamous but shows preferential chromosome pairing with complete restoration of fertility. The parental chromosomes are sufficiently differentiated and cleistogamy is either genic or due to gene-cytoplasm interaction but sterility is entirely chromosomal. All floral parts excepting calyx are highly deformed. Such a deformity is associated with sterility in the F_1 but with fertility in the amphidiploid. This is perhaps the first case of origin by hybridization of a true breeding and fully fertile cleistogamous taxon from two chasmogamous species. It also shows the extent and nature of change in breeding system brought about by hybridization and/or polyploidy.

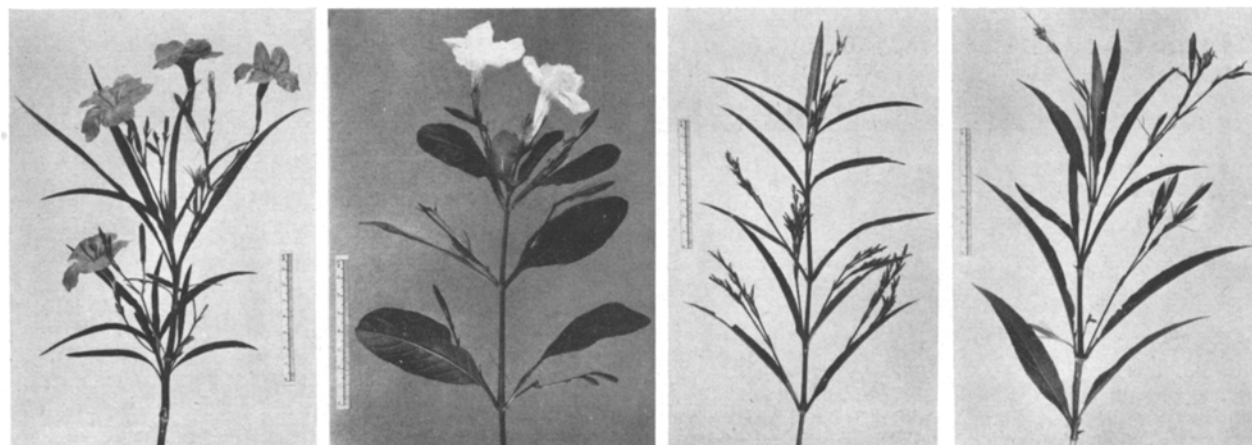
The chromosome numbers in the six, out of 16, obligate cleistogamous taxa (Table 4) show that they are high polyploids. Perhaps their origin has been in the same manner as in the present case.

Ruellia tweediana Griseb., a naturalized species from Argentina, and *R. tuberosa* Linn., distributed throughout the tropics, popularly known as "wild petunias", are among the few summer-flowering ornamentals in Lucknow. The two species were hybridized initially with the objective of enhancing variability in flower colour and form. However, far from being ornamental, flowers of the hybrid were very small which abscised early and had inconspicuous corolla. The present communication gives an account of the origin and inheritance of cleistogamy (obligate autogamy) in the parents, F_1 hybrid and amphidiploid together with the implications of the results.

Parents

Both the parents have large conspicuous chasmogamous flowers (Figs. 1, 2, 5 and 6). The flower

colour in *R. tweediana* is veronica-violet, while in *R. tuberosa* it varies from wistaria blue, white to white with pink base. Both species are self compatible and also cross pollinated by insects. Styles are long (Fig. 9) and may be exerted or at the level of stamens or even below them. When exerted, the distance between stigma and anthers does not preclude the possibility of self-pollination by insects. Furthermore, ephemeral corolla, while falling down, rubs anthers of epipetalous stamens against stigma; thereby even a totally isolated plant fruits normally. This is the mode of pollination every year from April to November. However, in December to January or February more than 85% flowers become cleistogamous. The two types of flowers, chasmogamous and cleistogamous, are irregularly distributed in inflorescences. Corolla in cleisto-



Figs. 1–4. Floral shoots of *R. tweediana* (Fig. 1), *R. tuberosa* (Fig. 2), F_1 (Fig. 3) and amphidiploid (Fig. 4). The former two have large chasmogamous, while the latter two have small and cleistogamous flowers. F_1 is totally sterile but amphidiploid is fully fertile

Table 1. Crossability between *R. tweediana* and *R. tuberosa*

Cross	Type	No. of flowers pollinated	Percentage fruit set	No. of seeds per capsule	Percentage germination
<i>R. tweediana</i> × <i>tweediana</i>	Self	10	100	15–24	90
<i>R. tuberosa</i> × <i>tuberosa</i>	Self	10	100	15–30	100
<i>R. tweediana</i> × <i>tuberosa</i>	F ₁	65	7.4	7–8	80
<i>R. tuberosa</i> × <i>tweediana</i>	F ₁	54	4.6	5–7 Shrunken and papery	Nil
F ₁ × <i>R. tweediana</i>	Backcross	33*	Nil	Nil	Nil
F ₁ × <i>R. tuberosa</i>	Backcross	31*	Nil	Nil	Nil

* Six chasmogamous flowers produced by the F₁ on June 29, 1965 were also utilized in this crossing.

gamous flowers is much reduced and remains included within calyx which is normal in size (Fig. 7). Both types of flowers fruit and fruits are distinguishable by the length of their styles (Fig. 8). In fruits from chasmogamous flowers, style is conspicuously longer than those from cleistogamous flowers. The difference in length of style is the result of normal corolla development in the former, in comparison to the highly arrested development in the latter in which case corolla is in the form of a small cap on the ovary itself. Thus the parents are predisposed for two types of flower development and breeding systems.

F₁ Hybrid (*R. tweediana* × *R. tuberosa*)

The two species were both selfed and reciprocally crossed and the results are summarized in Table 1.



Figs. 5–6. Complete flowers and corollas (from left to right) in *R. tweediana*, F₁, amphidiploid and *R. tuberosa*.

The fruit set, number of seeds per capsule and germination percentage is near normal in the parents, while in the hybrid combinations it is much lower and the two reciprocals differ significantly in this respect. Number of seeds from *R. tweediana* × *R. tuberosa* is about 50% of the normal seed production in the female parent, while in the reciprocal it is significantly lower. The seeds obtained in the former combination are well filled, but are shrunken and papery in the latter. About 80% seeds from the former while none from the latter combination germinate. There is thus a strong difference between the two reciprocals. The exact causes of this difference have not been ascertained so far.

The characters of the F₁ hybrids, *R. tweediana* × *R. tuberosa*, together with the parents have been summarized in Table 2. The general habit is more like the female parent. However, vegetative characters are qualitatively intermediate but quantitatively these exhibit a more luxurious growth (Fig. 3) in comparison to the parents. Flowers and floral parts reveal that except calyx all other parts remain highly underdeveloped (Fig. 5). Corolla is white with greenish-brown tip and forms a small closed canopy over the carpel (Fig. 6). Stamens and carpel also remain underdeveloped. Style is very small and stamens are situated just above the stigma which remains pressed against them (Fig. 9). The flowers of the F₁ are thus cleistogamous and more or less resemble the cleistogamous flowers of the parents produced in winter with the difference that in the parents such flowers are fertile, while in the F₁ they are sterile and fall off without producing any seed (compare Figs. 5 and 7). The F₁ hybrid has been under observation for the last 5 years and has remained cleistogamous and sterile.

Normal flowers were noticed in F₁ extremely rarely in the last week of June, 1965 and 1968. In both years they appeared in extremely low percentage, soon after the first premonsoon shower. Such chasmogamous flowers resemble the parents in size but did not yield any seed either after selfing or backcrossing with the parents (Table 1).

The present case is somewhat akin to the F₁ hybrids *R. occidentalis* × *R. humilis* and *R. occiden-*

Table 2. Summary of morphological characters

Species	<i>R. tweediana</i>	F_1 <i>R. tweediana</i> \times <i>tuberosa</i>	Amphidiploid <i>R. tweediana</i> - <i>tuberosa</i>	<i>R. tuberosa</i>
Chromosome No. (2n)	34	34	68	34
Habit	Erect	Erect, somewhat spreading	Erect	Decumbent
Height (cm.)	90	120	110	45
Leaf Shape	Linear	Oblanceolate	Oblanceolate	Broadly elliptic
L \times B (cm.)	15 \times 1.2	14 \times 2	16 \times 3.5	7.5 \times 2.8
Flower L \times B (cm.)	6 \times 3.5	1.5 \times 0.2	1.8 \times 0.35	5 \times 3
Calyx L \times B (mm.)	8 \times 2.5	10 \times 2	18 \times 3	25 \times 4
Corolla Colour	Veronica-violet	White with green apex	White with green apex	White
L \times B (cm.)	4.5 \times 3.5	0.45 \times 0.15	0.6 \times 0.25	5 \times 4.5
Stamens (mm.)	7-11	0.8	1.5	8-12
Pollen Stainable (%)	89.2	0	71	76.2
Size (μ)	56-80-92	24-47-68	73-82	48-76-96
Style (cm.)	2	0.15, somewhat coiled	0.2, somewhat coiled	2.2
Fruit (cm.)	2.2 \times 0.2	—	2 \times 0.35	2 \times 0.25
Seeds per fruit	15-24	—	13-18	15-30
Seeds L \times B (mm.)	2 \times 1.5	—	3 \times 2.9	2.5 \times 2

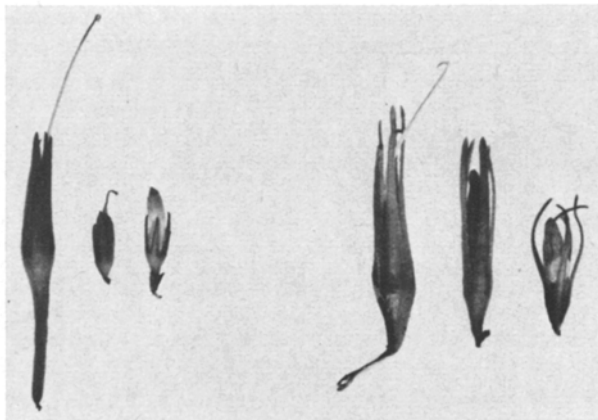
talis \times *R. brittoniana*. Both these hybrids are totally sterile. The former is reduced in vigour and produces cleistogamous flowers, while the latter is erect, vigorous and bushy but with numerous floral buds that abscise and rarely develop in cleistogamous flowers (LONG, 1966).

Amphidiploid (*R. tweediana-tuberosa*)

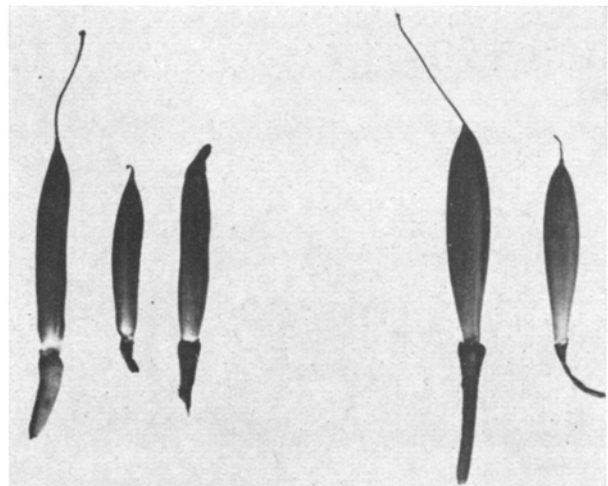
Vegetative buds of the F_1 hybrid were rendered polyploid by colchicine treatment. Such shoots also produced cleistogamous flowers which unlike F_1 did not fall off, but like the cleistogamous flowers in the parents produced normal capsules full of well-filled seeds. The seeds are larger than those of either of the

parents, and are perfectly germinable yielding C_1 amphidiploids which in turn gave true breeding C_2 and C_3 progeny.

The amphidiploid shows the general gigas characters associated with polyploidy (Table 2). The plants are sturdier, thicker, darker green and somewhat less luxurious in vegetative growth than F_1 (Fig. 4). The flowers though cleistogamous, are larger than F_1 (Fig. 5). Chasmogamous flowers have not been noticed so far in the amphidiploid. Like in the parents, cleistogamy in the amphidiploid affects the anther position rather favourably, which are situated just above the stigma that remains more often than not pressed against them because of a somewhat coiled style (Fig. 9).



Figs. 7-8. Chasmogamous (corolla removed) and cleistogamous flowers (Fig. 7) and fruits (Fig. 8) of *R. tweediana* and *R. tuberosa*. Note long style in chasmogamous while short style in cleistogamous flowers and fruits. $\times 1.5$ and $\times 1$



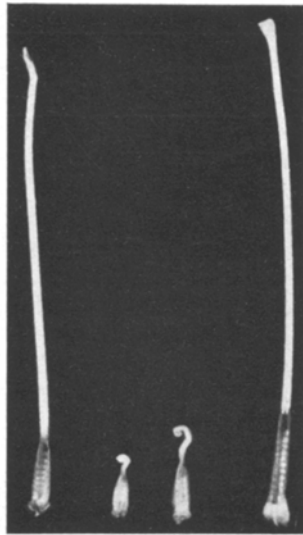


Fig. 9. Pistils (from left to right) in *R. tweediana*, F_1 , amphidiploid and *R. tuberosa*. Note long style in parents while significantly short and somewhat coiled style in the other two taxa. $\times 2.3$

Cytology

Acetocarmine squashes of pollen mother cells of the parents show that both have 17 bivalents at metaphase I followed by normal meiosis (Figs. 10 and 11). A large number of cells of F_1 hybrid ($2n = 34$) were analysed and the data are summarized in Table 3. While most cells possess bivalents and univalents, some cells contain associations of 3 or even 4 chromosomes. Some of the bivalents are rather heteromorphic (Figs. 12 and 13). Anaphases I and II are highly abnormal and are characterized by the presence of bridges mostly without fragments and dividing and lagging univalents (Fig. 14).

The higher frequency of pairs is evidently due to differential affinity between chromosomes of the two parents which, in absence of competition for pairing in F_1 , is enough to make them organise bivalents. The low frequency and rather loose associations of 3 or 4 chromosomes may not be of much significance and do not necessarily indicate interchange hybridity.

In the amphidiploid ($2n = 68$) there is almost complete bivalent formation, average per cell being 32.53 ± 0.43 (Table 3; Fig. 15). There is, however, a very low frequency of quadrivalents, trivalents and univalents in comparison to the F_1 hybrid from which it arose by chromosome doubling (Table 3). It is thus clear that in the amphidiploid bivalents are due to homogenetic or preferential pairing, while in F_1 they are heterogenetic or due to differential affinity. Furthermore, associations of more than 2 chromosomes in F_1 are not the result of any real or

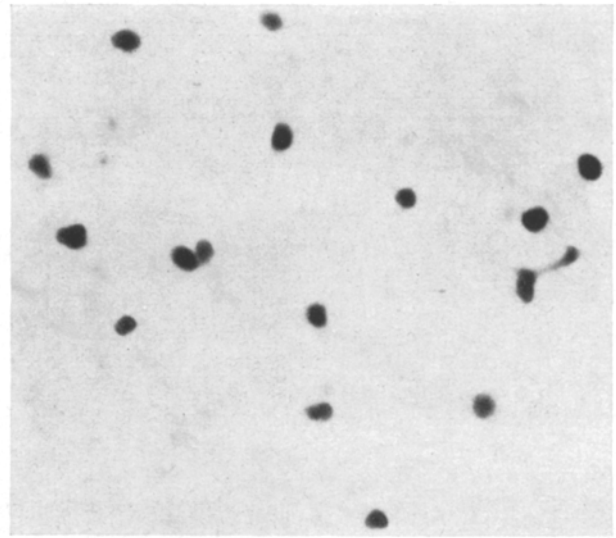


Fig. 10. *R. tweediana* 17 II. $\times 1560$

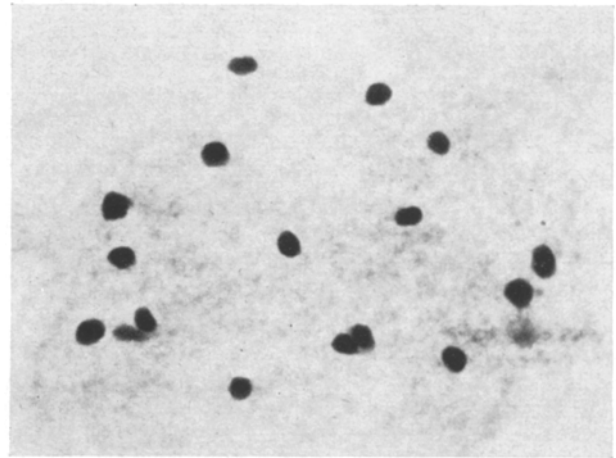


Fig. 11. *R. tuberosa* 17 II. $\times 1560$

extensive homology between parental chromosomes. Such associations may be pseudo-multivalents or some may even be accidental adherings. In contrast to the F_1 , anaphases in the amphidiploid are clean and normal.

Fertility

The parents are fully fertile, while F_1 , because of chromosomal abnormalities and segregational irre-

Table 3. Mean number and range of associations at M I

Taxon	Quadrivalents		Trivalents		Bivalents		Univalents	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
<i>R. tweediana</i>	—	—	—	—	17	17	—	—
<i>R. tuberosa</i>	—	—	—	—	17	17	—	—
F_1 (<i>R. tweediana</i> \times <i>R. tuberosa</i>)	1-3	0.36 ± 0.14	1-4	1.16 ± 0.25	5-17	11.04 ± 0.82	2-22	7.0 ± 1.05
Amphidiploid (<i>R. tweediana</i> - <i>tuberosa</i>)	0-1	0.06 ± 0.06	1-2	0.61 ± 0.19	29-34	32.53 ± 0.43	1-4	0.87 ± 0.32

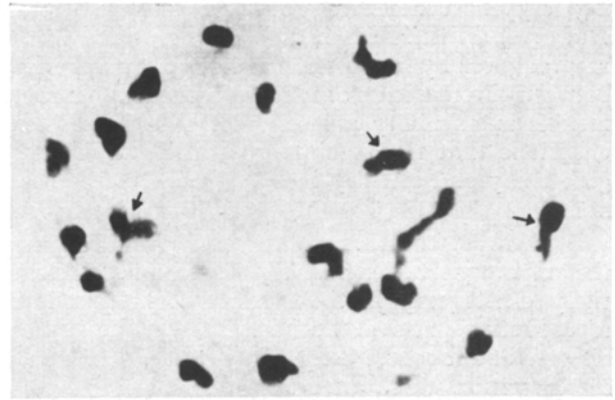
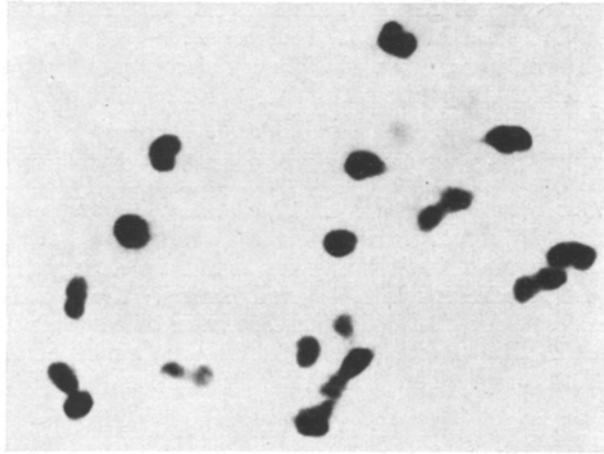


Fig. 12-13. F_1 , MI with 17 II and 16 II + 2I. Note heteromorphic bivalents. $\times 1560$

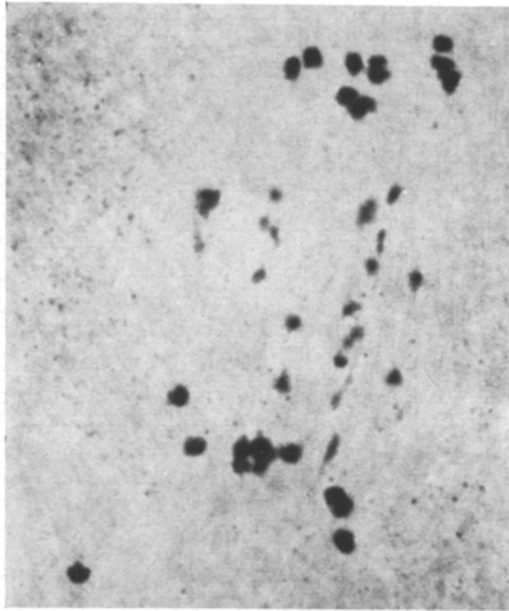


Fig. 14. F_1 , Anaphase I showing segregational irregularities. $\times 1560$

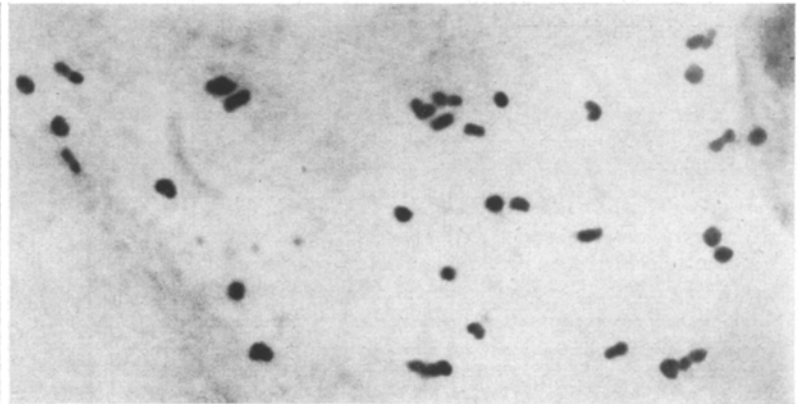


Fig. 15. Amphidiploid 34 II. $\times 1560$

gularities, is totally sterile even after backcrossing (Tables 1 and 2). In contrast to this, normal fertility was restored by suppression of recombination between the parental chromosomes in the amphidiploid although, like F_1 , it also possesses cleistogamous flowers (Table 2).

Discussion

R. tuberosa, one of the parents of the present F_1 hybrid, is among the first known examples of plant species producing cleistogamous flowers (UPHOR, 1938). In fact most species of the genus have a short cycle of cleistogamy but no taxon in the genus is reported to be exclusively cleistogamous like F_1 *R. tweediana* \times *tuberosa* and its amphidiploid, although *R. strepens* ($2n = 34$) is known to be strongly so. The latter has a short but ineffective chasmoga-

mous phase (LONG and UTTAL, 1962). It may be pointed out that cleistogamy is a regular feature in the annual cycle in most species of the genus *Ruellia*. Cleistogamous phase in the winter months in *R. tweediana* and *R. tuberosa*, and the rare chasmogamous flowers produced in F_1 in summers, are the result of gene-environmental interaction. However, it may be pointed out that far from being associated with sterility, as is the case in F_1 , cleistogamy is normally more effective in seed formation.

Pollen in F_1 is sterile and failure of backcrosses (Table 1) has shown that even the ovules are sterile. The total sterility is an indication of the wide genetic differentiation of the parents. Except in one more hybrid, *R. occidentalis* \times *R. brittoniana*, total sexual sterility and luxurious vegetative growth have not been found to go together in any intra- and inter-sectional *Ruellia* hybrid. The results of LONG (1966) have shown that the type of sterility found in the present F_1 hybrid is generally associated with very weak phenotype in *Ruellia*. He has also found a general lack of vegetative vigour in wide crosses. Pollen and ovule sterility in the present F_1 is entirely the result of reduced pairing, disharmonious recombinations between homoeologous chromosomes show-

ing cryptic differences and segregational errors. However, all these are immediately rectified in the amphidiploid by suppression of intergenomal pairing between chromosomes of the two parents and normal meiosis and fertility are restored. The logical conclusion is that the parents are sufficiently distinct genetically and sterility in F_1 is entirely chromosomal.

In contrast to other species, the present F_1 and the amphidiploid is exclusively cleistogamous. Essentially cleistogamy is the arrested development of reproductive parts of flowers. Here calyx is least affected and it covers the poorly developed and small corolla within which are included stamens and pistil which remain very small in size. This must be the result of some drastic change in physiological balance during the organogenesis of floral bud itself. It is evident that in F_1 such a situation is found throughout the year except for the very rare chasmogamous flowers in June. Furthermore, this condition is not rectified by polyploidy and accordingly chasmogamy is not restored in amphidiploid. Such a drastic change in flower size and structure often creates difficulty in taxonomic determination.

Cleistogamy cannot be confused with diplontic sterility because the former is actually telescoping of all the essential flower parts except calyx, while the latter is breakdown in normal development of the reproductive parts of flower. However, both cleistogamy and diplontic sterility are genically controlled and as expected are retained in amphidiploid condition.

The nature of genetic control and the exact location of this disharmony is not known at present. Whether cleistogamy in the F_1 and the amphidiploid is due to interaction between genomes of *R. tweediana* and *R. tuberosa*, or due to interaction between *tuberosa* chromosomes and *tweediana* cytoplasm, cannot be answered at present partly for want of the unsuccessful reciprocal hybrid, *R. tuberosa* × *R. tweediana*. At any rate, it appears that some genes controlling physiological balance essential for normal flower development are unable to carry out their functions. In the parents the normal functioning of such genes is also modified in winter resulting in cleistogamy. Similarly, the abnormal functioning in F_1 in the last week of June results in some chasmogamous flowers. It may be added that potentiality for cleistogamy already exists in the parents which is highly accentuated in hybrids. Perhaps between the two parental species they have all the factors responsible for a complete cleistogamous mode of flowering for which amphidiploid breeds true. That hybridity accentuates cleistogamy is also clear from LONG's (1966) observation on two hybrids, *R. occidentalis* × *R. brittoniana* and *R. occidentalis* × *R. humilis*, which are weak and cleistogamous. However, no case of a true breeding

cleistogamous *Ruellia* is known except the present amphidiploid *R. tweediana-tuberosa*.

The only other case of origin of cleistogamy through hybridization is the occurrence of rare individuals in the F_2 progeny of an interspecific hybrid, *Antirrhinum majus* × *A. glutinosum* (MATHER and VINES, 1951). Here cleistogamy is not found in the parents. Thus between the two parental *Antirrhinum* species there is latent genetical make up for cleistogamy. The requisite recessive genes found in the species were recombined in 0.43% individuals. The genetical basis for cleistogamy in *Antirrhinum* involves a minimum of 2 recessives in the primary genotype of cleistogamy. The inheritance is rather complex since some genes with supplementary action are apparently necessary for cleistogamous development but others modify its grade. In the cleistogamous types there is poor seed set due to inheritance of self incompatibility from *A. glutinosum* together with true hybrid sterility. Cleistogamous individuals breed true although there is very little self progeny. Such is not the case with cleistogamous taxa in general. However, cleistogamous *Antirrhinum* hybrids are different from the present case because the former arose in two steps i.e. F_1 followed by reshuffling of chromosomes giving rise to rare recombinants with appropriate gene combinations. In the present case, cleistogamy arose in a single step in F_1 itself and was maintained thereafter in the amphidiploid.

From the above discussion it emerges that the present amphidiploid (*R. tweediana-tuberosa*) is the only known fertile true breeding cleistogamous taxon that has arisen in experiment. The restoration of fertility is the result of polyploidy but normal seed set has been aided by the favourable mechanical adjustments for autogamy because stamens dehisce and deposit pollen grains on stigma itself.

The chasmogamous/cleistogamous cycle found in various species of *Ruellia* (LONG and UTTAL, 1962; LONG, 1964, 1966; present investigation) tallies with outbreeding/inbreeding system. The balance between the two types of breeding systems regulates recombination level. It is in the chasmogamous outbreeding phase that spontaneous F_1 hybrids arise between *R. tweediana* and *R. tuberosa* of which there is a large number of individuals already growing in this Garden. Vegetative reproduction helps to conserve all types of progeny ensuing after chasmogamous and cleistogamous cycles.

Against the above background of origin of a true breeding cleistogamous taxon, the hitherto reported cases of cleistogamy reviewed by UPHOF (1938) and McLEAN and IVIMEY-COOK (1956) can be classified into two chief categories.

The first is non-genetic, modificative or environmental cleistogamy which is often caused by contradictory environmental and other factors like water, drought, low or high temperature, light, soil

nutrition, etc. Adverse environment is the usual cause of such cleistogamy. For plants normally flowering in summer, cleistogamy is seen in autumn and winter, and vice versa. Furthermore, environmentally induced cleistogamy is a fertility insurance. As observed by CHASE (1908), in *Stipa* and *Danthonia* axillary cleistogamous flowers at the base of the plant, set seed under conditions of drought or heat. In this category cleistogamy may not be inherited but tendency to produce cleistogamous flowers under adverse condition may be heritable.

are known in otherwise chasmogamous species (Table 4). In all these cases, cleistogamy is a taxonomic character of specific or varietal identification.

It is of some interest to note that out of the 16 obligate cleistogamous taxa reported so far, chromosome number has been reported for 6 species (Table 4). It may be more than a coincidence that all the 6 are polyploid. This point may be of some significance when considered against the background of the origin of the present synthetic obligate cleistogamous amphidiploid taxon, *R. tweediana-tuberosa*. Perhaps

Table 4. *Chromosome number in cleistogamous taxa*

Name of the species	Chromosome number			Reference*
	x	n	2n	
<i>Cardamine chenopodiifolia</i>	7, 8, 15	—	64	MANTON, 1932
<i>Leersia oryzoides</i>	12	—	48	TATEOKA, 1954
		—	60	HIRAYOSHI, 1937
<i>Polycarpon tetraphyllum</i>	9	—	54	BLACKBURN and MORTON, 1956
<i>Salvia cleistogama</i>	6—11, 13,	—	64	DELESTAING, 1954
	17, 19	16	—	LINNERT, 1955
<i>Subularia aquatica</i>			ca. 36	LÖVE and LÖVE, 1956
<i>Calanthe veratrifolia</i> var. <i>cleistogama</i>	20	20	40	ARORA, 1960; PANCHO, 1965
Unworked Taxa: <i>Appendicula cleistogama</i> , <i>Bulbophyllum cleistogamum</i> , <i>B. scrobiculilabre</i> , <i>Chloreae inconspicua</i> , <i>Dendrobium cleistogamum</i> , <i>Liparis cleistogama</i> , <i>Panicum chapmani</i> , <i>Purpurella cleistiflora</i> , <i>Thelasis capitata</i> , <i>Plocoglottis glaucescens</i> var. <i>cleistogama</i> .				

* Data from DARLINGTON and WYLIE, 1955; CAVE et al., 1955—64; ORNDUFF, 1967 and 1968.

The second category is genetic cleistogamy in which the genotype is predisposed for facultative or obligate cleistogamy. Such taxa breed true for this character.

In the facultative cleistogamous plants both cycles go side by side and the best examples are the genera like *Commelina*, *Ruellia*, etc. UPHOF (1938) has shown that chasmogamous cleistogamous dimorphism is a constant character of *Commelina virginica*. When he grew uprooted plants in a damp jar without soil and subjected to sunlight, the aerial stems produced normal chasmogamous flowers while subterranean rhizomes continued to produce cleistogamous flowers even though they were in air. *Ruellia strepens* is another facultative cleistogamous taxon in which cleistogamy is more successful so much so that the cleistogamous phase was given a rank of variety (*R. strepens* Linn. var. *cleistantha* Gray) or a forma (*R. strepens* Linn. forma *cleistantha* (Gray) S. MCCOY). However, studies of LONG and UTTAL (1962) have shown that both phases exist on one and the same individual.

In obligate cleistogamy, chasmogamous flowers are either non-existent or are formed very rarely. Well known cases of this category are listed in Table 4. ASCHERSON (1871) cultivated successive progenies of *Salvia cleistogama* for 5 years and found it to breed true. Even well established cleistogamous varieties

in all these cases the events leading to the establishment of obligate cleistogamy may be similar which may now be enumerated in brief.

Genes for cleistogamy may be in a latent or unexpressed state in species in which the character may manifest only under different environmental conditions. Two such species may have between them the complete genetic make up for full expression of the character and if they are otherwise sufficiently differentiated genetically, they are likely to produce genically cleistogamous but chromosomally sterile hybrid. The former alters the positional relation of various essential organs favourably, resulting in stamens being situated immediately above stigma borne on a coiled style by which it remains pressed against stamens. Under such circumstances even the rare production of unreduced gametes can be advantageous in production of a fertile polyploid. It is in cleistogamous taxa that GRANT'S (1956) hypothesis about the easy origin of polyploids in self pollinated plants can come in full play. Furthermore, such a taxon because of cleistogamy itself could be efficiently isolated from its parents. In this way the chances of stabilization of a fertile cleistogamous taxon are very high.

Hybridization, polyploidy and cleistogamy may be correlated in the same manner as in apomixis (see STEBBINS, 1950). Such an interpretation does

not in any way minimize the role of mutation in the origin of cleistogamy as advocated by BURCK (1906). In fact the first initiation has to be through mutation, hybridization only helps to bring together appropriate gene combinations required to start a cleistogamous cycle and polyploidy suppresses the breakdown and stabilizes the whole system. Like apomixis (GUSTAFSSON, 1947), cleistogamy may be induced by favourable gene combinations in diploids, but it seems to be accentuated at polyploid level.

It may also be pertinent to mention that a correlation of obligate cleistogamy and polyploidy as hinted here is basically in consonance with such a correlation between inbreeding and polyploidy already discussed by GRANT (1956), STEBBINS (1957) and BAKER (1959).

LONG (1964) has pointed out that in South Florida *Ruellias* are outbreeding cross fertile taxa and show a continuous variation as is expected of allogamous species. He further states that absence of polyploidy in *Ruellia* supports this view as many cross fertile groups tend to be diploid and inbreeders are frequently polyploid. In this connection it may be of interest to mention that we have in our cultures a natural tetraploid (34 bivalents) chasmogamous species of *Ruellia*, which according to authorities at Kew is related to *R. tuberosa*. Furthermore, the effect of cleistogamy on overall structure of populations and evolutionary potentialities of taxa in question would be the same as obligate inbreeders. The rare outcrossing in obligate chasmogamous inbreeders is also rendered possible in obligate cleistogamous taxa through the production of rare chasmogamous flowers.

In conclusion, it may be pointed out that the present case has shown the way by which two partially cross pollinated species can give rise to an obligate inbreeding taxon in one step through institution of cleistogamy. Furthermore, cleistogamy could also be an excellent isolating mechanism needed for the survival and stabilization of the new taxon.

Zusammenfassung

Ruellia tweediana und *R. tuberosa* sind großblütige, chasmogame Diploide ($n = 17$) mit normaler Meiosis und Fertilität. Die F_1 -Hybriden, die nur in einer Richtung gelingen (*R. tweediana* \times *R. tuberosa*), sind vegetativ kräftig und besitzen häufig 17 heteromorphe Bivalente mit einem hohen Anteil an Spaltungsunregelmäßigkeiten. Die Hybride ist ausschließlich kleistogam und vollkommen pollen- und samensteril. Wie die F_1 ist auch die künstlich hergestellte Amphidiploide ($n = 34$) kleistogam und zeigt eine präferentielle Chromosomenpaarung mit völliger Wiederherstellung der Fertilität. Die elterlichen Chromosomen sind genügend differenziert. Die Kleistogamie ist entweder genisch bedingt oder auf eine Gen-Cytoplasma-Interaktion zurückzuführen, die Sterilität ist ausschließlich durch die Chro-

mosomen verursacht. Alle Teile der Blüte mit Ausnahme der Calyx sind stark deformiert. Bei der F_1 ist diese Deformation mit Sterilität verbunden, die amphidiploide Form ist jedoch fertil. Das ist vielleicht der erste Fall eines aus der Kreuzung zweier chasmogamer Spezies hervorgegangenen reinerbigen und voll fertilen kleistogamen Taxons. Es läßt sich auch der Umfang und die Art der durch Hybridisierung und durch Polyploidie verursachten Änderung des Zuchtsystems erkennen. Die Chromosomenzahl bei 6 von 16 obligaten kleistogamen Taxa (Tab. 4) zeigt, daß sie hochpolyploid sind. Vielleicht sind sie auf eine gleiche Weise wie im vorliegenden Falle entstanden.

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