# GENETIC BARRIERS IN THE COSMANTHUS PHACELIAS (HYDROPHYLLACEAE)<sup>1</sup>

## GEORGE W. GILLETT

The Cosmanthus phacelias occur in North America from Guatemala to New York State and total 14 recognized species (Constance, 1949). Eleven of these occur northeast of the Texas Gulf Coast over an extensive region in which no other phacelias are indigenous. This group, therefore, has a notable degree of geographic unity.

The appearance of additional work on the Cosmanthus phacelias might seem redundant to those who recall the revisions accorded them by Gray (1875), Brand (1913), and Constance (op. cit.). However, the last revision was followed by a paper (Constance, 1950) that stressed three putative hybrid phylogenies within six species of the group and urged their investigation by breeding experiments. The current paper presents and summarizes a crossing program carried out with these six species and four additional ones in the Cosmanthus group.

The chromosome number is known for thirteen of the fourteen species in this group (Cave and Constance, 1947, 1950). Of the ten species in the crossing program, eight, *Phacelia fimbriata* Michx., *P. gilioides* Brand, *P. hirsuta* Nutt., *P. laxa* Small, *P. patuliflora* (Engelm. & Gray) A. Gray, *P. platycarpa* (Cav.) Spreng., *P. purshii* Buckl., and *P. strictiflora* (Engelm. & Gray) A. Gray, are characterized by nine pairs of chromosomes. Two species, *P. dubia* (L). Trel.; and *P. maculata* Wood, have five pairs.

The four excluded species are: *Phacelia bipinnatifida* Michx.; *P. glabra* Nutt.; *P. pulcherrima* Const.; and *P. ranunculacea* (Nutt.) Const. Each is a very distinct taxon. *Phacelia bipinnatifida* has the not-unusual chromosome complement of nine pairs, but a disparity in chromosome number is noted for *P. glabra* (8 pairs) and *P. ranunculacea* (14)

<sup>&#</sup>x27;Aided by grants from the National Science Foundation.

pairs). No chromosome information is available for *P. pul*cherrima, a comparatively rare Mexican endemic.

Plants of the following races were grown from seed in the greenhouse at East Lansing. Races of *Phacelia hirsuta*, *P. gilioides*, *P. strictiflora*, *P. patuliflora*, *P. dubia*, and *P. maculata* were also grown at Turku, Finland.

Species	$Seed \ Locality$	Documented $by^2$
P. strictiflore	aDallas Co., Texas	Gillett 1257
P. patuliflord	a San Patricio Co., Texas	Gillett 1216
P. laxa	San Patricio Co., Texas	Gillett 1217
P. platycarpe	aVolcan Tacana, Guatemala	Beaman 3200
	Nevada de Toluca, Mexico	Gillett 1252
P. hirsuta	Washington Co., Arkansas	Gillett 1215
P. gilioides	Osage Co., Missouri	Gillett 1260
P. purshii	Sevier Co., Tennessee	Gillett 1214
	Butler Co., Ohio	Gillett 1203
P. fimbriata	Swain Co., North Carolina	Gillett 1207
	Sevier Co., Tennessee	Gillett 1213
P. maculata	Lancaster Co., South Carolina	Gillett 1208
P. dubia	Dare Co., North Carolina	Gillett 1262

Some species of *Phacelia* are protandrous (with the anthers dehiscing before the stigmas are receptive), so that a seed-set is rarely obtained by pollinating newly-opened flowers. Consequently, flowers of proposed ovulate parents were emasculated just before anther dehiscence, labeled with a jeweler's tag, and pollinated two days later. Self-pollinations by this method produce viable seed in all species, so that the experimental cross-pollinations provide reliable tests of genetic compatibility. Stigmas were examined by a  $15 \times$  hand lens to verify their freedom from contaminating pollen before experimental cross-pollinations were made.

Capsules from cross-pollinated flowers were harvested at dehiscence and placed in storage for approximately three months. Products from a given cross, including seeds with obviously retarded development, were then placed on stand-

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<sup>&</sup>lt;sup>2</sup>Voucher specimens deposited at the Herbarium of the University of California, Berkeley.

ard germination paper in a petri dish and moistened with 0.2% KNO<sub>3</sub>, a solution that produces favorable germination in these species. Petri dishes were covered and placed in a growth chamber with alternating periods of 20° centigrade (16 hours) 30° (8 hours). Upon germination, seedlings were planted in a mixture of equal parts of screened sand and peat in 3-inch clay pots. These were watered from below until cotyledons emerged and expanded.

All of the species were studied in native habitats, and the variability of each species was studied by the examination of several hundred herbarium specimens.<sup>3</sup>

The comparative morphology of seeds and glandular trichomes has provided helpful guides to evolutionary relationships in *Phacelia* (Gillett, 1960), so that it was appropriate to study the seeds and trichomes of the Cosmanthus group. Seed morphology, including seed size and shape, seed coat sculpturing, and embryo form and size, was determined for all species. Glandular trichromes were studied from whole mounts of living material.

All these species are self-fertile, and all are outcrossers except *Phacelia purshii* which is self-pollinated. The results of breeding experiments are presented in Table 1, the data summarized in terms of the number of ovules tested in the seed parents. The number of seeds produced by self-pollinated flowers of the seed parent was taken as a reasonably conservative approximation of the number of ovules available for cross-fertilization. The number of seeds per capsule was determined as the median complement of seeds from 5 to 30 capsules.

The experimental crosses were made to determine genetic affinities and to test channels of potential gene flow among the 10 species in the group. All 45 potential channels have

<sup>&</sup>lt;sup>3</sup>Appreciation is extended to herbarium curators at the Chicago Natural History Museum; Gray Herbarium of Harvard University; Michigan State University; Missouri Botanical Garden; New York Botanic Garden; Smithsonian Institution; University of California, Berkeley; University of Michigan; University of Texas; and the University of Wisconsin for making herbarium specimens available for this study.

been tested, 39 of these by reciprocal crosses. Of the possible combinations, only the one between *Phacelia hirsuta* and *P. gilioides* was found conclusively to permit gene flow. Fertile  $F_1$  and  $F_2$  hybrids were obtained from this cross. It must be emphasized that the genetic barriers indicated in Table 1 are relative and not necessarily absolute. They may restrict gene flow, but may not be capable of stopping it completely, especially if large numbers of flowers are cross-pollinated in the natural habitat.

Seed morphology contributes significant evidence of relationships in this group. The uniformly larger, keeled seeds of *Phacelia fimbriata* and *P. purshii* are consistently distinguishable from the much smaller, angular to ovoid seeds of the other species in the group. The uniformly larger seeds of *P. fimbriata* are distinguishable from those of *P. purshii* in mixed samples.

The remaining eight species can be classified into two groups on the basis of seed characters: those species in which the seed coat sculpturing is registered on the endosperm (recognizable with a hand lens), including Phacelia patuliflora, P. strictiflora, and P. laxa; and those species in which the seed coat sculpturing is not registered on the endosperm, including P. platycarpa, P. dubia, P. maculata, P. gilioides, and P. hirsuta. The seeds of P. patuliflora, P. strictiflora and P. laxa are similar in size, shape (angular to ovoid), and seed coat design (Fig. 1, a, b). These three species have a common chromosome number, occur in the same region, and have other morphological similarities that suggest a common evolutionary line. In the second group, seeds of P. platycarpa are distinguished by a relatively large embryo, over 1 mm. long (Fig. 1, h). Seeds of the remaining four species P. dubia, P. maculata, P. gilioides, and P. hirsuta are remarkably similar in size, shape (angular), seed coat design, and embryo morphology (Fig. 1, c, d, j, k). However, the disparity in chromosome number between P. dubia and P. maculata (n = 5), on the one hand, and P. gilioides and P. hirsuta (n = 9), on the other, suggests that these similarities in seed are expressions of parallel evolution in two distinct lines.





Fig. 1. a-k. Longi-sections of seeds showing endosperm sculpturing and embryo morphology: a, *Phacelia patuliflora*, *Gillett 1216*; b, *P. strictiflora*, *Gillett 1257*; c, *P. hirsuta*, *Gillett 1215*; d, *P. gilioides*, *Gillett 1260*; e, *P. laxa*, *Gillett 1217*; f, *P. fimbriata*, *Gillett 1207*; g, *P. purshii*, *Gillett 1214*; h, *P. platycarpa*, *Beaman 3200*; j, *P. maculata*, *Gillett 1208*; and k, *P. dubia*, *Gillett 1262*.

The glandular trichomes, or colleters, of all ten species are characterized by unicellular heads and uniseriate stalks, a type found in several other phacelias.

Field studies and the examination of extensive herbarium collections have provided supporting evidence for most of the genetic barriers indicated in the crossing program. Six of these species, including *Phacelia dubia*, *P. fimbriata*, *P. laxa*, *P. maculata*, *P. platycarpa*, and *P. purshii*, are in each instance distinct from other phacelias. While each of these has its own range of variability, I have found no indication that this is caused by hybridization with any other species.

Intermediates between *Phacelia gilioides* and *P. hirsuta* occur frequently in nature, and have been produced from experimental crosses. Variability of the natural hybrids is so extensive as to effect a complete intergradation between the two species. In nature, these portray a single, genetically isolated complex.

The two remaining species, *Phacelia patuliflora* and *P. strictiflora*, also blend into each other through intergrading forms. These is evidence, therefore, that natural hybridization has occurred between these species even though it was not possible to secure experimental hybrids. This suggests that the internal genetic barrier is relatively weak and is easily bridged when sufficient numbers of flowers are crosspollinated in nature. These two intergrading species also appear to constitute a genetically isolated complex.

The three hybrid phylogenies cited by Constance (1950) are listed below.

PARENT	PUTATIVE HYBRID	PARENT
1. P. strictiflora var. lundelliana	P. strictiflora var. robbinsii	P. hirsuta
2. P. patuliflora var. teucriifolia	P. patuliflora var. patuliflora	P. laxa
3. P. hirsuta	P. gilioides	P. purshii

The first problem cited above involves variable and intergrading races of *Phacelia strictiflora*. The race of *P. strictiflora* grown in this study would correspond more nearly to Cosmanthus — Gillett

var. lundelliana. No hybrids were obtained in the limited crosses between this material and P. hirsuta seed parent, and studies of herbarium material revealed no natural hybrids between P. strictiflora and P. hirsuta. Several herbarium collections include mature seed. Variability in seed structure in no way suggests gene flow into P. strictiflora from P. hirsuta, or in the reverse direction. Seed differences between these two species are qualitative rather than quantitative. A similar qualitative difference is noted in the calyx whch is accrescent in P. strictiflora and non-accrescent in P. hirsuta. In summary, the results of this study indicate that P. hirsuta has not contributed genes to the highly variable P. strictiflora.

The second problem involves highly variable and intergrading races of *Phacelia patuliflora*. The race of *P. patuli*flora grown in this study would correspond most nearly to var. patuliflora. Extensive crosses from P. laxa to the P. patuliflora seed parent produced no hybrids, and sufficient ovules were tested to have revealed a very low compatibility, if such exists. Therefore, a relatively effective genetic barrier is indicated between the putative hybrid (P. patuliflora var. patulifora) and one of its proposed parents (P. laxa). Phacelia laxa is sympatric with P. patuliflora, its distribution falling entirely within the range of the latter, and populations of the two species grow in close proximity in nature. However, I was unable to detect natural hybrids in herbarium material. Ecological, morphological, and genetical differences between these species would indicate that they have evolved independently of each other for some time.

The proposed hybrid origin of *Phacelia gilioides*, with P. hirsuta and P. purshii as parental lines, is strongly suggested by corolla morphology for the crenulate-fimbriate corollas of P. gilioides seem clearly intermediate between the entire corollas of P. hirsuta and the strongly fimbriate corollas of P. purshii. However, the study of several differences, including seed characters, long-recognized to be among the most conservative in *Phacelia*, revealed qualitative differences between P. purshii, on the one hand, and P. gilioides

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Races of *Phacelia platycarpa*, *P. purshi*, and *P. fimbriata* are *Beaman 3200*, Gillett 1214, and Gillett 1213, respectively.

				POLLEN	PAR	ENT				
		<i>u</i>	0							,
S E E D	ctiflora	patuliflora	laxa	platy carpa	hirsuta	gilioides	purshii	fimbriata	maculata	dubia
P A R E N T										
strictifiora (7)		14	7	0	0	0	0	0	0	7
patulifiora (11)	22	I	396	33	22	22	22	22	44	22
laxa (6)	12	54		18	9	9	12	12	24	9
platycarpa (3)	9	9	9	Ι	9	9	9	9	9	9
hirsuta (7)	28	14	14	21		28*	63	14	14	14
gilioides (5)	15	10	10	10	50*		20	15	10	10
purshii (4)	20	8	8	8	36	20	I	20	80	8
fimbriata (4)	12	8	∞,	12	16	12	20	I	80	∞
maculata (7)	14	28	42	14	14	28	21	21	Ι	84
dubia (5)	10	15	20	10	20	10	10	10	85	I

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and *P. hirsuta* on the other. These qualitative differences are correlated with experimentally demonstrated internal genetic barriers. Additional evidence of the genetic integrity of *P. purshii* is seen in its inbreeding system which tends to reinforce, rather than to overcome, the internal genetic barrier. The study of herbarium material and of populations in nature has produced no evidence that the variability of *P. purshii* is caused by gene flow from *P. gilioides*, or that the variability of *P. gilioides* and *P. hirsuta* is related to gene flow from *P. purshii*. Available evidence suggests that *P. purshii* is in a distinct evolutionary line and that *P. gilioides* and *P. hirsuta* constitute another.

Crossing programs completed on 23 diploid species of *Phacelia*, involving at least five major evolutionary lines (Sections WHITLAVIA and GYMNOBYTHUS, the *P. franklinii* group, *P. linearis* (a monotypic line), and the Cosmanthus group) indicate that speciation in this genus usually involves an internal genetic barrier. Where no internal genetic barrier has evolved, other barriers are relatively weak, always permitting crossing in nature, presumably through the inconstant behavior of insect pollinators. Where taxonomic problems occur in these five groups (and there have been five such cases), they have been traceable to natural hybridization.

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### CHROMOSOME COUNTS FOR PASPALUM<sup>1</sup>

### DONALD J. BANKS

I have made some additional chromosome counts during my studies in the genus *Paspalum*. None of the counts for the taxa reported herein, except *P. laeve*, are recorded in the Chromosome Atlas (Darlington and Wylie, 1955) or in the Index to Plant Chromosome Numbers (Cave, 1956-1962). My counts of n = 40 for *P. laeve* are different from 2n = 40which was reported by Brown (1948).

The counts were made from pollen mother cells squashed in aceto-carmine after fixation in alcohol-acetic acid (3:1). Photomicrographs were made of cells with chromosomes distributed so that they were countable. Drawings, made by tracing enlargements of the photomicrographs, are presented in Figures 1-5.

<sup>&</sup>lt;sup>1</sup>Contribution No. 55 from the Stephen F. Austin State College Department of Biology. Part of this work was done at the University of Texas Department of Botany while I was a National Science Foundation research participant during the summer of 1963. Thanks are due Dr. W. V. Brown for providing facilities during the research period.



Fig. 1-5. Meiotic chromosomes of species of Paspalum. Fig. 1. P. blodgettii. Fig. 2. P. caespitosum. Fig. 3. P. fimbriatum. Fig. 4. P. fluitans. Fig. 5. P. laeve.

The voucher specimens are deposited in the Herbarium of Stephen F. Austin State College. The chromosome numbers obtained are presented below:

Ρ.	Species	Voucher Specimen	n
	blodgettii Chapm.	FLORIDA: Dade Co., 3.2	20
Ρ.	caespitosum Flügge	miles s. of Florida City, Banks 1246 FLORIDA: Collier Co., 6 miles n. of Rock Island, Banks 1198	20

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P. fimbriatum H.	B. K. FLORIDA: Monroe Plantation Key 1223	Co., 10 , Banks
P. fluitans (Ell.) H	Kunth TEXAS: Nacogdoc 5 miles s. and 7 e. of Cushing, B	hes Co., 10 .2 miles <i>Canks 1910</i>
P. laeve Michx.	GEORGIA: Clarke Athens, Banks	Co., 40 1053
	TEXAS: Nacogdoc Stephen F. Aus perimental For Banks, 1913	hes Co., 40 tin Ex- rest,

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## SOME OBSERVATIONS ON THE DISSEMINATION OF TRIPSACUM

## WALTON C. GALINAT AND FRANK C. CRAIGHEAD

The observations reported here on the dissemination of Tripsacum are the results of a continuing attempt to uncover more information on this grass which might shed additional light on its evolutionary relationship with maize. In particular, we were interested in Tripsacum floridanum because it has certain features which are primitive for the genus. It is endemic to south Florida and crosses more easily with maize than do most other species of Tripsacum (Galinat, 1961). Since our previous collections of T. floridanum had all been from Dade County and chiefly in the Everglades National Park, we set out to botanize for this grass in Collier County, an area of greater geological age than that of Dade County.

On our trip westward along the Tamiami Trail in Collier County, we were able to make our first observations. They suggested water as a factor in the spread of Tripsacum. The relationship between the highway and a canal along one side, created by the road construction technique used in south Florida, made possible these observations. While we were driving westward, the canal lay on our side of the highway and, after a few checks for accuracy, we began to count colonies of T. dactyloides, while traveling at a speed of at least 40 miles per hour, slower speeds being hazardous on this highway. The characteristic clumps of plants with arching, rather broad grass leaves together with scattered tall flowering canes bearing tassel-like inflorescences enabled us to identify this plant with ease and rapidity. In one 25 mile long strip, we observed in this manner about 25 colonies of Tripsacum. On the return trip along the same length of highway but on the other side which lacked an abutting canal, we observed only one colony of Tripsacum. It seemed possible that flotation along the canal, perhaps during periods of high water, had a role in spreading the

*Tripsacum* on the canal side and, thereby, resulted in its higher frequency there.

Other observations suggesting that water is involved in the spread of Tripsacum came from the distribution of T. floridanum, the prime object of our trip to Collier County. This species is most frequently located at the margin of the slightly higher limestone where it protrudes into the marl land which characterizes the glades. It would seem that the Tripsacum fruit cases float across the usually flooded glades and become established on the out-cropping of limestone which forms pine hammocks. The Tripsacum usually does not migrate far into the pine land from its beach head, unless the undergrowth, such as saw palmetto, is sparse, and unless the canopy is sufficiently open to permit penetration of diffuse to full sunlight.

With these field observations in mind, we went to the laboratory and readily demonstrated that the mature grainbearing fruit cases of Tripsacum did, indeed, have this essential capacity to float on water. In this experiment, thirty-three fruit cases were spilled out into a beaker full of water. They immediately began to float, and during the following week only about a quarter of them sank, as shown in Table I.

Table I. The floating capacity of mature fruit cases of *Tripsacum* dactyloides.

Days on water	Percent floating
0	100
1	94
2	85
3	82
4	76
5	73
6	73

Slight differences in the tightness with which the cupule wings clasped the outer glume of the enclosed spikelet, differences in the density of hairs in the pulvinus notch through which water may enter and differences in the shape and thickness of the rachis segment appear to have affected the floating capacity of the fruit cases. If we assume that a good floating capacity had some selective advantage as a means of dispersal, then the structure of the fruit cases may have been altered along these lines.

We have also made a few observations on factors other than water which seem to be involved in the spread of Tripsacum. During the few stops that we made along the Tamiami Trail drive, we noted that the seasonal mowing of the banks by the State Highway Department seemed to stretch the colonies out, as if by dragging from the mowers moving parallel to the banks. This mowing, furthermore, seemed to aid the growth of *Tripsacum* by temporarily eliminating competition for light by other plants which made a slower recovery from being cut back.

Fire, like the mowing, likewise seems to be important in keeping an area sufficiently open for Tripsacum, at least in the case of T. floridanum on pine land. The rhizomes of T. floridanum are fairly fire-resistant and a regrowth of its shoots is frequently the first sign of green in a fire-blackened area. The numerous, tightly packed leaf bases of Tripsacum usually protect the growing points on the rhizomes from destruction by fire. Furthermore, the burning off of some of the mass of dead, usually wet, leaf bases seems to stimulate new growth from the axillary buds. The sprouting of these buds may stem from both the physical removal of enclosing dead tissue as well as the removal of an unfavorable chemical environment immediately around the growing points.

Another most interesting means of dispersal of Tripsacum came to light in a story related to us by a farmer, Mr. Glenn Simmons. Mr. Simmons was quite familiar with T. floridanum, in that a large growth of it occurs in the pines around his farm. He said that the local inhabitants frequently carried a pocket full of the fruit cases to chew when out on hunting trips in the Everglades. The fully matured Tripsacum fruit cases which are much too hard to chew were sometimes cracked open with the teeth and the grain shelled out for eating. But if the mature fruit cases were either swallowed whole or just discarded to the ground, they might became effectively dispersed. At least in the case of teosinte, Garrison Wilkes (unpub.) reports that cattle do pass the fruit cases through the digestive tract and that the seed recovered from the manure remains viable. Man is known to have chewed teosinte for a considerable period of time. The senior author has identified fragments of a teosinte fruit case in human coprolites from Romero's Cave in Tamaulipas, carbon-dated at  $3650\pm250$  years (E. O. Callen, personal communication).

The possibility that birds such as ducks may be involved in the dispersal of Tripsacum has also been considered. Experiments are contemplated for testing this by feeding Tripsacum fruit cases to chickens or domestic ducks and then spreading the recovered dung out on the ground where any viable fruit cases may germinate.

In the case of teosinte, the indigo bunting, certain grosbeaks and sparrows in Guatemala consume the seed by shelling it out of the fruit case. The result is a complete digestion and destruction of the seed (Stadelman, 1939).

Isolated plants and small colonies of Tripsacum are occasionally found far removed from presently existing glades or other water sources. These exceptional plants may have been transported to such places by other means or else they may represent relic survivors from ancient distributional patterns.

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