Pl. Syst. Evol. 133, 29—37 (1979)

Plant Systematics and Evolution

From the Department of Botany, University of Texas, Austin

The Pollination Spectrum in the Southwestern American Cactus Flora*

By

Verne Grant and **Karen A. Grant,** Austin

(Received November 25, 1978)

Key Words: *Cactaceae.*—Flower pollination.

Abstract: The cacti of the American Southwest, defined as the region from southern California to Texas, are surveyed for types of pollination systems and their frequencies. Four types of pollination systems are known to occur in the southwestern cactus flora: bee, hummingbird, hawkmoth, and bat pollination. Two other modes are suspected but not documented: miscellaneous small-insect pollination and autogamy.—Bee flowers comprise a wide and nearly continuous series of size classes from very small to very large. The large bee flowers, with perianths 5.5 to 12.5 cm in diameter, form a prominent but arbitrarily delimited subcategory in the bee pollination system. Promiscuous flowers and autogamous flowers, if they occur, are included with the medium-sized and small bee flowers in our present classification, due to lack of information, and will have to be separated out when our knowledge is more complete. The overwhelming majority of species in the southwestern cactus flora are bee flowers. Between 39 and 44% of the species are large bee flowers. Another 50 to 56% of the species are classified as medium-sized and small bee flowers; while some of these may turn out to be promiscuous flowers and autogamous flowers, most of them are undoubtedly bee flowers.—Hummingbird, hawkmoth, and bat pollination are conspicuous but statistically minor components of the pollination spectrum, occurring in only one or a few species (see Table 2). Hummingbird pollination has arisen from bee pollination in the Southwest. The species or species groups with hawkmoth and bat pollination, on the other hand, are basically tropical groups which developed their advanced pollination systems in the tropics.

The pollination spectrum of a plant group or phytogeographical region is described by the types of pollination systems and their frequency distribution. This paper is a first attempt to portray the

* Pollination of North American Cacti, V. See also GRANT & GRANT (1979a), GRANT & al. (1979), GRANT & GRANT (1979b), GRANT & HURD (1979).

0378-2697/79/0133/0029/$ 01.80

pollination spectrum of the cacti in the American Southwest. The evidence now available is sufficient for such a first attempt. However, it is necessary to realize that there are large gaps in the evidence which will have to be filled in by future studies.

PORSCH (1938, 1939) recognized five main pollination systems in the family *Cactaceae* as a whole. These are: bee flowers, promiscuous flowers (Blumen mit gemischtem Besucherkreis), hummingbird flowers, hawkmoth flowers, and bat flowers. All of these systems are present in the southwestern cacti, but their frequencies are very unequal.

The terms—bee flowers, bat flowers, etc.—as used here do not imply exclusiveness. We mean that the primary adaptations of the flowers are to a given class of pollinating agents. Other classes of agents may visit the flowers too but play a secondary role.

The American Southwest is defined for our present purposes as the region from southern California to Texas. The taxonomy of the cacti of this region has been worked out by BENSON (1969a, 1969b, 1969c). This provides a necessary foundation for comparative pollination-ecological studies.

Bee Flowers and Promiscuous Flowers

The floral syndrome of large, diurnal, colorful, bowl-shaped flowers with numerous petals and stamens is widespread in southwestern cacti, occurring commonly in *Opuntia*, *Echinocereus*, and other genera, and is associated with pollination by medium-sized and large bees.

PORSCH's (1938) category of promiscuous flowers (Blumen mit gemischtem Besucherkreis) has the following syndrome. The flowers are diurnal, medium-sized to small, radiate or disc-shaped, with numerous stamens, and having a variously colored perianth (white, yellow, pink, etc.). The nectar is not buried in a floral cup or tube but is easily accessible to short-tongued insects, and the pollen is also readily accessible. PORSCH (1938) cites examples from *Pereskia*, *Lophophora*, *Rhipsalis*, and other genera.

PORSCH included some medium-small bowl-shaped flowers in his list of examples of promiscuous flowers, thus broadening the definition of this category, but we believe that a restricted definition of promiscuous flowers is more useful. Our line of thought is as follows.

Large bee flowers and promiscuous flowers do not form distinct classes. The one type grades into the other through a third intermediate class of medium-small, diurnal, bowl-shaped flowers. Such flowers are common in the southwestern cacti, occurring in some species of *Mammillaria*, *Opuntia*, and other genera.

The intergradation in flower size can be demonstrated by taking the

Table 1. Frequency distribution of perianth sizes in southwestern cacti

Normal maximum perianth diameter in species, cm	No. species in Arizona cactus flora	No. species in Texas cactus flora
0.5	1	3
1.0	1	3
1.5	1	1
2.0	3	2
2.5	7	6
3.0	7	7
3.5	1	—
4.0	6	3
4.5	1	3
5.0	11	10
5.5	3	2
6.0	1	10
6.5	7	1
7.0	1	—
7.5	9	8
8.0	3	2
8.5	—	—
9.0	3	1
9.5	—	—
10.0	—	2
10.5	—	—
11.0	—	—
11.5	—	—
12.0	—	1
12.5	1	2
(No data)	—	(2)
Total	67	69

normal maximum perianth diameter for each species as given in taxonomic descriptions. This has been done for the cactus floras of Arizona and Texas on the basis of BENSON's (1969a, 1969c) treatments. The results are shown in Table 1. There is an essentially continuous series from very small to quite large flowers in the two floras. Under these conditions the distinction between large and small flowers is an arbitrary one. We have found it convenient to draw the arbitrary dividing line between 5.0 and 5.5 cm.

Most of the small and medium-sized flowers are bowl-shaped, while relatively few are radiate or disc-shaped, in the southwestern cacti and indeed in the family as a whole. There are intermediate conditions between bowl-shape and disc-shape, depending on the angle of spread

of the perianth segments, but the two types can usually be recognized in their extreme conditions.

We suggest, therefore, that the array of flower size and form variations could be grouped into three rather than two intergrading categories. These are: large bowl-shaped flowers, medium sized to small bowl-shaped flowers, and medium or small disc-shaped flowers.

The large bowl-shaped flowers are now known to be pollinated by medium-sized and large bees in a number of representative species [*Echinocereus fasciculatus* (ENGELM.) L., *Ferocactus wislizenii* (ENGELM.) BR. & R.; *Opuntia lindheimeri* ENGELM., etc.] (GRANT & GRANT, 1979a, 1979b; GRANT & al. 1979; GRANT & HURD 1979). The modes of pollination in the smaller bowl-shaped flowers and disc-shaped flowers have not been investigated. The medium-sized and small bowl-shaped flowers are probably also bee flowers.

PORSCH (1939) made the plausible prediction that the pollinators of the disc-shaped flowers would consist of a wide range of small insects, particularly short-tongued bees, flies, wasps, and small beetles. This prediction is, in general, consistent with what is known about flowers with this syndrome outside the *Cactaceae* (see KNUTH, 1906-1909; KUGLER, 1970, pp. 197ff.; etc.). However, direct observational evidence for disc-shaped flowers in the *Cactaceae* is much needed. PORSCH's category of disc-shaped promiscuous flowers is in many respects the most poorly known pollination class in the *Cactaceae*.

It should be noted that some disc-shaped flowers, for instance those in *Opuntia fulgida* ENGELM., are probably bee flowers (GRANT & HURD 1979). The possibility should also be kept in mind that some very small and inconspicuous flowers, such as those in *Epithelantha*, may turn out to be autogamous or partially so.

It is interesting that fly flowers, which are well developed in the cactus-like stapeliads of Africa, are absent among the cacti of the Southwest and indeed in the family as a whole (FAEGRI & VAN DER PIJL 1971, p. 119). We formerly thought that beetles were important pollinators of southwestern cacti, but this conclusion has not stood up under further investigation (see GRANT & HURD 1979).

Bird, Moth, and Bat Flowers

Red tubular hummingbird flowers are fairly common in the cactus floras of the Andean and other tropical American regions (PORSCH 1937, 1939). By contrast, this pollination system is very uncommon in the American Southwest. It occurs here in only one species, *Echinocereus triglochidiatus* ENGELM. (GRANT & GRANT 1967). Even this may be an

overestimate. More extensive investigation of *Echinocereus triglochidiatus* may well reveal that it is not exclusively hummingbird-pollinated but is a facultative bird-and-bee flower.

The hawkmoth-flower syndrome, consisting of strongly-scented night-blooming flowers with white or whitish perianths and long slender nectar-containing floral tubes, is present in *Cereus*, *Trichocereus*, *Selenicereus*, *Discocactus*, *Epiphyllum*, and a number of other cactus genera (PORSCH 1939). Few pollination records are available for these plants; PORSCH cites one case involving cultivated *Cereus jamacaru* DC. and native *Phlegethontius sexta* JOH. in a botanic garden in Chile. Enough is known about the distinctive flower syndrome in other plant families, however, to justify reliable predictions in the cacti.

There are two species of *Cereus* in the Southwest with the hawkmoth-flower syndrome. These are *Cereus pentagonus* (L.) HAW. (*Acanthocereus p.*) and *Cereus greggi* ENGELM. (*Peniocereus g.*). Both species have floral tubes 10 cm long or longer. Both species occur in Texas and one of them (*C. greggii*) occurs also in Arizona. *Cereus pentagonus* is a wide-ranging tropical American species which barely gets into southern Texas; it is therefore only a marginal member of the southwestern cactus flora. Needless to say, pollination records should be sought for this and other hawkmoth-flowered cacti.

The bat-flower syndrome is characterized by large, nocturnal, whitish, bowl-shaped flowers, with unpleasant odors and abundant nectar. PORSCH (1939) first called attention to the occurrence of this syndrome in the *Cactaceae*. VOGEL (1968), in a critical review, finds that bat flowers are widespread in tropical and subtropical members of the tribe *Cereeae*, where they occur in some 37 genera and about 160 species.

MORAN (1961, 1962) has obtained a bat pollination record in the *Cactaceae* in nature. He found *Pachycereus pringlei* (S. WATS.) BR. & R. being visited and pollinated by bats in southern Baja California. Birds and insects play a secondary role in pollination.

The cactus flora of the American Southwest contains three species of bat flowers. These are: *Carnegiea gigantea* (ENGELM.) BR. & R., *Lemaireocereus thurberi* (ENGELM.) BR. & R. (*Stenocereus t.*), and *Lophocereus schottii* (ENGELM.) BR. & R. In the American Southwest all three species occur in Arizona and *Carnegiea* extends into extreme eastern California.

Experimental tests with caged plants confirm the prediction of bat pollination for *Carnegiea gigantea* (ALCORN & al. 1959; MCGREGOR & al. 1962) and for *Lemaireocereus thurberi* (ALCORN & al. 1962). The bat species involved in the tests is the glossophagine bat *Leptonycteris nivalis*, which is undoubtedly a principal pollinator in nature. Birds and bees also visit the flowers in nature.

Pollination Spectrum

The percentage frequencies of the various pollination systems in southwestern cactus floras are given in Table 2. We do not have the information at present to estimate the frequency of disc-shaped promiscuous flowers. This class of flowers is grouped with the small and medium-sized bee flowers. This grouping does not distort the picture very much since the disc-shaped promiscuous flowers are probably bee-

Table 2. Frequency of different pollination systems in three southwestern cactus floras

Pollination System	No. and % of species in cactus flora of:					
	Arizona		Texas		S. California	
	No.	%	No.	%	No.	%
Large bee flowers	27	40.3	27	39.1	15	44.1
Medium and small bee flowers*	35	52.2	39	56.5	17	50.0
Hummingbird flowers	1	1.5	1	1.4	1	2.9
Hawkmoth flowers	1	1.5	2	2.9	—	—
Bat flowers	3	4.5	—	—	1	2.9
Total	67		69		34	

* May include a contingent of promiscuous flowers and autogamous flowers; see text.

pollinated to a substantial extent anyway. Of course, as noted earlier, it is desirable to seek more direct evidence concerning disc-shaped flowers in the *Cactaceae*. The advanced pollination systems (bird, moth, and bat pollination) did not present a comparable problem because these classes are well defined.

We see in Table 2 that the cactus floras of Arizona, Texas, and southern California consist preponderantly of bee flowers (including an unknown small contingent of promiscuous flowers). The advanced pollination systems in these floras, though interesting and conspicuous, represent only minor elements statistically in their respective floras. The southern California cactus flora is the poorest of the three in these advanced pollination systems.

It is interesting to look at a tropical American cactus flora for comparison. The cactus flora of Jamaica is useful for this purpose

because it is a geographically discrete entity, has been treated taxonomically (by FAWCETT and RENDLE 1926), and has been studied from the standpoint of hummingbird flower visits (by LACK 1976).

Table 3 gives the percentage frequency of the various flower classes in Jamaican cacti. We see, as expected, a much higher proportion of hummingbird and hawkmoth flowers than in the southwestern cactus floras.

Table 3. Frequencies of different flower classes in the cactus flora of Jamaica. [Based on data in FAWCETT and RENDLE (1926) and LACK (1976)]

Pollination System	No. species	%
Promiscuous flowers (in *Rhipsalis*)	3	20.0
Bee flowers (in *Opuntia*, *Pereskia*)	5	33.3
Hummingbird flowers (in *Nopalea*, *Melocactus*)	2	13.3
Hawkmoth flowers (in *Cereus*)	4	26.7
Bat flowers (in *Stenocereus*)	1	6.7
Total	15	

Discussion

The most primitive type of flower in the *Cactaceae* is that found in the primitive genus *Pereskia*. As exemplified by *P. aculeata* (PLUM.) MILL. and other species, the flowers are day-blooming, medium-sized, radiate or disc-shaped, with numerous stamens, and a variously colored perianth (white, yellow, pink, etc.). They could be either bee flowers or promiscuous flowers.

The bowl-shaped bee flowers which are so common in the American Southwest are about one evolutionary step removed from the open disc-shaped type of flower, and are probably derived phylogenetically from it. The large bowl-shaped flowers in this region are probably products of parallel evolution where they occur in the separate tribes, *Opuntieae* (*Opuntia*) and *Cereeae* (*Ferocactus*, *Echinocactus*, *Echinocereus*, etc.). Bee pollination is obviously a very successful pollination system in the Southwest and has been adopted by numerous cactus species belonging

to different tribes and genera. The Southwest is a region rich in native bee species (HURD 1978).

The one species of hummingbird flower in the Southwest (*Echinocereus triglochidiatus* ENGELM.) occurs in a predominantly bee-flowered genus and represents another evolutionary step, in this case away from bee pollination. It is not clear why there are not more hummingbird flowers in the cacti of the Southwest.

The hawkmoth-flowered and bat-flowered cacti of the Southwest represent a different situation in which Mexican and other tropical American floristic elements have extended into the Southwest. This is the case in the two hawkmoth-flowered species of *Cereus*, and particularly in *Cereus pentagonus* (L.) HAW. which is widespread in tropical America and only marginally present in our area.

It is also the case in the three species of columnar cacti with bat flowers in Arizona. GIBSON, who has made a phylogenetic study of the large columnar cacti, finds that the Arizona species are the end-points of separate lines which come together in groups in southern Mexico today (GIBSON 1978, and personal communication). Hawkmoth and bat pollination have not evolved to any considerable extent in the southwestern cactus flora, but have entered this flora from more southern areas.

This study was supported by National Science Foundation Grant DEB 76-81274.

References

ALCORN, S. M., MCGREGOR, S. E., BUTLER, G. D., KURTZ, E. B., 1959: Pollination requirements of the saguaro (*Carnegiea gigantea*). — Cactus Succulent J. **31**, 39—41.

— MCGREGOR, S. E., OLIN, G., 1962: Pollination requirements of the organpipe cactus. — Cactus Succulent J. **34**, 134—138.

BENSON, L., 1969a: The Cacti of Arizona; ed. 3. — Tucson: University of Arizona Press.

— 1969b: The Native Cacti of California. — Stanford: Stanford University Press.

— 1969c: *Cactaceae*. — In LUNDELL, C. L.: Flora of Texas **2**, 221—317. — Renner (Texas): Texas Research Foundation.

— WALKINGTON, D. L., 1965: The southern Californian prickly pears—invasion, adulteration, and trial-by-fire. — Ann. Missouri Bot. Garden **52**, 262—273.

BRITTON, N. L., ROSE, J. N., 1963: The *Cactaceae*; ed. 2, reprint. — New York: Dover Publications (Original printing of edition 2 in 1937).

FAEGRI, K., PIJL, L. VAN DER, 1971: The Principles of Pollination Ecology; ed. 2. — Oxford and New York: Pergamon Press.

FAWCETT, W., RENDLE, A. B., 1926: Flora of Jamaica **5**, 271—286. — London: British Museum.

GIBSON, A. C., 1978: Systematic anatomy and phylogeny of Mexican columnar cacti. — Ann. Missouri Bot. Gard., in press.

GRANT, K.A., GRANT, V., 1967: Records of hummingbird pollination in the western American flora, III. — Aliso **6**, 107—110.
GRANT, V., GRANT, K.A., 1979a: Pollination of *Echinocereus fasciculatus* and *Ferocactus wislizenii*. (Pollination of North American cacti, I.) — Pl. Syst. Evol. **132**, 85—90.
— — 1979b: Pollination of *Opuntia basilaris* and *O. littoralis*. (Pollination of North American cacti, III.) — Pl. Syst. Evol. **132**, 321—325.
— HURD, P. D., 1979: Pollination of *Opuntia lindheimeri* and related species. (Pollination of North American cacti, II.) — Pl. Syst. Evol. **132**, 313—320.
— HURD, P. D., 1979: Pollination of the Southwestern Opuntias. (Pollination of North American cacti, IV.) — Pl. Syst. Evol. **133**, 15—28.
HURD, P.D., 1978: Superfamily *Apoidea*. — In KROMBEIN, K.V., & al. (Eds.): Catalog of *Hymenoptera* in America North of Mexico **2**. — Washington, D.C.: Smithsonian Institution Press.
KNUTH, P., 1906—1909: Handbook of Flower Pollination. 3 vol., translation. — Oxford: Clarendon Press.
KUGLER, H., 1970: Blütenökologie; ed. 2. — Stuttgart: Gustav Fischer Verlag.
LACK, D., 1976: Island Biology; Illustrated by the Land Birds of Jamaica. — Berkeley: Univ. California Press.
MCGREGOR, S.E., ALCORN, S.M., OLIN, G., 1962: Pollination and pollinating agents of the saguaro. — Ecology **43**, 259—267.
MORAN, R., 1961: Visitantes de las flores de *Pachycereus pringlei*. —Cactaceas (Mexico) **6**, 94—96.
— 1962: Visitors to the flowers of *Pachycereus pringlei*. — Cactus Succulent J. **17**, 21.
PORSCH, O., 1937: Die Bestäubungseinrichtungen der *Loxanthocerei*. — *Cactaceae*, Jahrb. Deutsch. Kakteen-Gesellsch. **1937**, 15—20.
— 1938: Das Bestäubungsleben der Kakteenblüte, I. — *Cactaceae*, Jahrb. Deutsch. Kakteen-Gesellsch. **1938**, 1—80.
— 1939: Das Bestäubungsleben der Kakteenblüte, II. — *Cactaceae*, Jahrb. Deutsch. Kakteen-Gesellsch. **1939**, 81—142.
VOGEL, S., 1968: Chiropterophilie in der neotropischen Flora, Neue Mitteilungen I. — Flora (B) **157**, 562—602.

Address of the authors: Dr. VERNE and KAREN A. GRANT, Department of Botany, University of Texas, Austin, TX 78712, U.S.A.