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Reproductive Systems in *Chelone glabra* var. *glabra*¹

T. S. COOPERRIDER²

Abstract. The results of a series of experiments and field observations indicate that bumble bees are the chief pollinators of *Chelone glabra* L. var. *glabra*, but that their activity may lead frequently to geitonogamy and less often to xenogamy. Flowers from which corollas were removed failed to attract bees and did not produce seed. Flowers that were unaltered but shielded from insect visitation also failed to produce seed. Seeds were produced on plants cross-pollinated by hand. Seeds were also produced after pollination of stigmas with pollen from their own inflorescence. This facultative geitonogamy is likely a contributing factor to the geographical distribution pattern of the variety, a pattern characterized by relatively isolated colonies.

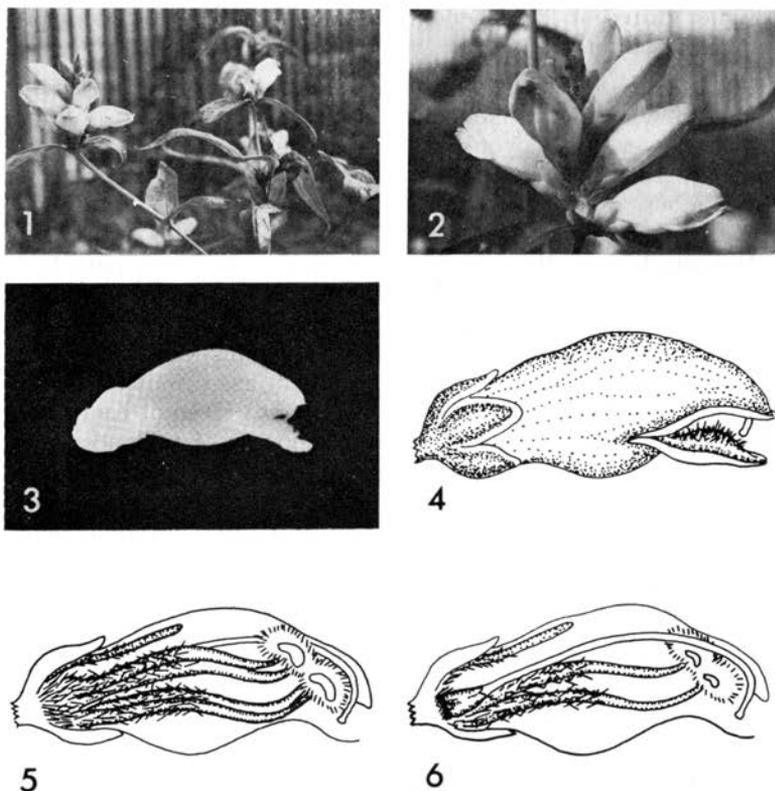
Pennell (1, p. 177) observed that the corolla of the genus *Chelone* "is admirably fitted by size and form for pollination by bumble bees". During the summer of 1966, a series of experiments were conducted on the reproductive system in *Chelone glabra* L. var. *glabra*. The results combined with field data suggest that while bumble bees are the chief pollinating agents, their activity may lead frequently to geitonogamy, and less often to xenogamy.

The taxon is distributed in eastern North America from Newfoundland west to Ontario and Minnesota and south to Georgia and Missouri. Observations of plants throughout much of this range indicate that it is rarely—if ever—an abundant element in any flora. Rather it tends to occur in somewhat isolated colonies. Plants within the colonies are seldom contiguous, and often are widely scattered.

Insect activity around colonies of *Chelone glabra* var. *glabra* in northeastern Ohio, was observed on several occasions. Bumble bees were the most frequent visitors and the only large insects entering deeply into the flower and brushing against both stigma and anthers. *Chelone* pollen was recovered from the hairs on the dorsum of the thorax and from pollen baskets on the hind tibiae. The bees apparently seek the secretion of the nectaries at the base of the ovary. Rarely a bee lands on top of the flower and, inverted, enters the distal part to collect pollen. In foraging, a bee tends to work one area intensively, entering each opened flower from one to several times before moving to another site. Individual plants have several inflorescences (Figure 1), each with more than one flower open at a time (Figure 2). If the plant is separated from others by a distance of even one or two feet, the bee tends to confine its activity to the flowers of one plant at a time,

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Figures 1-6. *Chelone glabra* var. *glabra*. Figure 1. Upper part of plant showing several inflorescences. Figure 2. Inflorescence. Figure 3. Photogram of flower. X1. Figure 4. Flower. Figure 5. Androecium and gynoecium. Figure 6. Same, with two near anthers removed to show gynoecium.

thus promoting geitonogamy. However, no selectivity among the various plants was apparent on the part of the bumble bees. In one instance where a branch of *Lobelia siphilitica* L. touched a branch of *Chelone*, a bumble bee went back and forth from one to the other entering flowers of each repeatedly.

When a bee moves from one *Chelone* plant to another, the possibility of xenogamy occurs. Even here, however, the result may in some cases be a form of inbreeding. Vegetative reproduction by fragmentation of the rhizome is easily accomplished in cultivation. It is likely that in places where wild plants are contiguous or nearly so, the individuals have often resulted from vegetative reproduction. As observed by Faegri and van der Pilj (2, p. 25), pollen transfer from one such individual to another is classed as xenogamy in studies of pollination ecology. Genetically, however,

it is not different from geitonogamy; and both are genetically equivalent to autogamy.

Chelone glabra var. *glabra* produces a zygomorphic flower the corolla of which is sympetalous but two-lipped distally (Figure 3). The lower lip is covered with matted hairs and forms a landing place for bees (Figure 4). The androecium consists of four didynamous, epipetalous stamens and a staminode (Figure 5). The filaments of the two shorter stamens lie in the upper part of the corolla tube, those of the two longer in the lower part. Distally, all curve upward in such a way that the two pairs of anthers are within the upper lip. The four anthers are not connate, but are held together at maturity by masses of tangled hairs that originate from the anther wall. The anthers are oriented so that the lines of dehiscence are on the contiguous faces of each pair. This results in the dropping of large amounts of pollen on any object which pries them apart. The superior ovary is surrounded basally by a ring of nectaries. The style lies between the two upper filaments. As it matures, the style develops a terminal bend or hook finally bringing the stigma to a position in front of, and somewhat below, the four anthers (Figures 5 & 6).

As the bee enters the flower and moves toward the nectaries, its body touches the stigma and the matted hairs on the lower lip. It moves between the right and left anthers of each pair, forcing them apart, and bringing the sides of dehiscence into contact with its back.

Experiments were carried out with plants dug from several localities in northeastern Ohio and established in clay pots in a research garden in Kent. Wild plants in a colony a few miles distant served as controls. Several factors affecting pollination were varied. In each case, the purpose was to determine whether or not seed would be produced under the conditions imposed. Seed production proved to be either abundant or completely lacking. (Table 1).

In all cases of positive seed set, a sample of 10 seeds gave 100% germination after soaking for a few days in 0.01% gibberellic acid.

Some plants (2a-b) were grown inside an open lath house where several bumble bees visited daily. Some flowers were left unaltered. From others the corolla and androecium were removed prior to anther dehiscence, leaving only the gynoecium and the calyx.

Other plants (3a-e) were placed on a low platform and covered with screen cages. These were subjected to the several conditions listed in the table.

In the case of plants caged with bees (3e), new bees were introduced on several different days during the flowering season.

Table 1. Seed Production Under Various Conditions

1. Wild plants	Seed Set abundant
2. Plants in open lath house	
a. flowers unaltered; no hand pollination	abundant
b. corolla and androecium removed; no hand pollination	none
3. Plants in screen cages	
a. flowers unaltered; no hand pollination	none
b. corolla and androecium removed; no hand pollination	none
c. corolla and androecium removed; cross-pollinated by hand (xenogamy)	abundant
d. corolla and androecium removed; hand-application of pollen from same inflorescence (geitonogamy)	abundant
e. caged with bumble bees; no hand pollination	abundant

They remained active at most for but a few hours. After flying against the screen for some time, they began visiting flowers in a somewhat lethargic manner. Each finally remained in a flower and died there.

The failure of seed to be produced in 2b suggests that as with *Mimulus* (3) bagging of flowers will be unnecessary in cross-breeding experiments. That these corolla-less flowers did not attract bees was further borne out by the accumulation of large amounts of nectar which seeped out between the calyx lobes.

The production of seeds in 3c and 3d indicates the effectiveness of hand-pollination. The failure of seed set in 3a where otherwise unaltered flowers were shielded from insect visitation points to the obligate dependence of plants in the wild on insect pollination. The increasing curvature of the style as the flower ages does not lead to autogamy. Nevertheless, the production of seeds in 3d, coupled with the observed tendency of a bee to visit several flowers of the same plant consecutively, suggests that in the wild geitonogamy is more apt to occur than xenogamy.

This facultative geitonogamy would have enabled pioneers to establish colonies in suitable habitats at considerable distances from other stands of *Chelone*. This is likely a major contributing factor to the present distribution pattern which is characterized by relatively isolated colonies distributed over a wide geographic range.

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