POLLINATION SYNDROMES IN THE GENUS ECHINOCEREUS: A REVIEW*

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Flowering plants with highly specialized floral structures and complex floral designs—such as orchids and asclepiads—depend entirely on a particular pollinator. In contrast, some families (e.g., the Cactaceae) in most cases have flowers with simple floral morphology, and their pollination can be achieved by more than one pollinator. Insects, birds, and mammals make up part of the pollination spectrum of the Cactaceae (Rowley, 1980; Porsch, 1939).

The following information is a general overview of the pollination syndromes in the genus *Echinocereus*, based on previous literature. Additionally, in trying to better understand the process of evolution of the genus, the possible mechanisms leading to speciation events in the genus are discussed.

Members of the Cactaceae display a wide variety of flowers both in shape and size. In addition to the beauty of their flowers, the unusual and characteristic vegetative morphology of these plants has attracted the attention of both amateurs and specialists, making cacti an essential part of many living collections. However, studies of reproductive biology, in particular breeding systems, in the Cactaceae are few and poorly documented.

In general, cacti are outcrossers, which leads to maximum genetic variability in the progeny due to genetic recombination of parental genotypes (Gibson and Nobel, 1986). Other breeding systems have been reported to occur among the members of the family, although they are uncommon. Self-compatibility or autogamy occurs in Lophophora and Arthrocereus (Rowley, 1980). Cleistogamy has been reported in species with small flowers, such as in Frailea and Melocactus, enforcing self-pollination (Rowley, 1980; Gibson and Nobel, 1986). Although there has been some misunderstanding of the sexual condition of the family, monocliny is the usual sexual condition. Dioecy—a rare sexual condition in cacti—has only been documented in three species of *Opun*tia, namely O. stenopetala, O. grandis, and O. glaucescens (Parfitt, 1985). Vivipary (germination of seeds before they are shed from the parent plant) occurs in Epiphyllum phyllanthus (Conde, 1975), Coryphantha vivipara (Zimmerman, 1985), and in some species of *Rhipsalis* (Wallace, pers. comm.). Gynodioecy has been cited in *Mammillaria dioica* (Ganders and Kennedy, 1978; Parfitt, 1985) and *M. neopalmeri* (Parfitt, 1985), but is believed to represent functional dioecy. Finally, functional dioecy has been observed in some populations of *Echinocereus coccineus* (Parfitt, pers. comm.). In these species, morphologically hermaphroditic flowers appear to be functionally staminate, although further investigations are needed.

On the other hand, facultative asexual reproduction is common and might represent an advantage in colonizing new habitats. In sexual reproduction, cacti usually produce many seeds, but the establishment of seedlings is low.

The structure of the cactus flower displays several features related to adaptations for dry environments and different modes of pollination. Cacti usually bloom in spring, although certain species flower in different seasons of the year (Bravo, 1978). Mature flowers are usually showy, colorful and fully open, displaying stamens and stigma to potential pollinators. The ovary is inferior, a feature of highly specialized groups such as orchids, sunflowers and irises (Gibson and Nobel, 1986; Richards, 1986), and embedded in stem tissue which in turn protects developing ovules from desiccation.

In the Cactaceae, there is a tendency toward characteristics which promote outcrossing. Herkogamy, the spatial separation of stigma and stamens, is the usual condition in cactus flowers, and with the various floral syndromes, serves to promote cross fertilization. The cacti, as in many outcrossing species, are highly dependent on biotic pollinators to disperse their pollen. So far, no wind pollinated species have been documented in this group. The floral syndromes reported to occur in the Cactaceae involve the following vectors: bees, birds (hummingbirds and doves), mammals (bats), and lepidopterans (hawkmoths). A fifth category has been described as promiscuous flowers, e.g., flowers that do not exhibit preference for a particular pollinator (Porsch, 1939; Grant and Grant, 1979b; Rowley, 1980). These biotic pollination syndromes are related to floral morphology, including functional structures, such as stigma, stamens, pollen, shape and size of the flower, time of opening (diurnal or nocturnal), amount of nectar and pollen production, presence or absence of scent, etc. (Faegri and Van der Pijl, 1979; Grant and Grant, 1979b).

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Bee pollination is the most common pollination system in cacti and is considered to be the primitive condition. Grant and Grant (1979b) report that in the pollination spectrum of the cactus flora of the southwestern U.S., the occurrence of species with large to medium size pollinators is high (93.5%) compared with bird, bat, and moth pollinated cacti (6.5%). Bird, bat, and hawkmoth pollinations, all derived conditions, are less common and tend to occur in some tribes (e.g., Pachycereeae, Trichocereeae) of the cactus flora of Central and South America, from where they have evolved into the North American flora (Gibson and Nobel, 1986; Grant and Grant, 1979b; Wallace, pers. comm.).

In bee or other insect pollination, the color, size, and shape of the flower are part of its attributes, and are of particular importance because they function as long-distance signals to attract pollinators. Therefore, floral attributes, including nectar guides and pollen production, serve to help insects obtain rewards and help the plants to reproduce sexually (Kevan, 1978), and hence promote genetic variation.

Several cases of bee pollination within the Cactaceae have been documented, e.g., Grant and Grant (1979a, 1979b) and Grant, Grant and Hurd (1979). Flowers of *Echinocereus fasciculatus, Ferocactus wislizenii* and several *Opuntia* species are visited by different species of bees of various sizes. Nevertheless, medium to large bees are the most successful pollinators. Additionally, experimental tests on pollination of saguaro (*Carnegiea gigantea*) flowers demonstrate that this species exhibits a wide pollination spectrum and adjusts to different pollinator agents. In fact, cross-pollination is achieved by bees and doves as well as by bats, which are the most efficient pollinators (McGregor et al., 1962).

Grant and Grant (1979a), Grant, Grant and Hurd (1979), and Grant and Hurd (1979) at first considered that beetles were part of the pollination spectrum of the Cactaceae. Further detailed studies, e.g., Grant and Connell (1979), led to the conclusion that even though several types of beetles are common visitors to cactus blossoms, they do not pollinate these flowers. This association is related to the reproductive cycle of beetles, since oviposition and larval development take place in the floral parts. Indeed, beetles restrict their activity to the stamens and filaments, and visits to different flowers, in particular to the stigmas, are infrequent. Thus, if pollination occurs, it occurs accidentally.

It seems that the extended phenology of some cactus flowers is related to secondary adaptations to additional pollinators. These secondary adaptations might be massive production of pollen and the relatively long period of anthesis, allowing several types of pollinators to visit, as in *Carnegiea gigantea* (McGregor et al., 1962). Also, the open morphology of the cactus flower, and

thus the presentation of both stigma and stamens, may even facilitate casual pollination.

Floral Biology and Pollination Syndromes in *Echinocereus*

Species of *Echinocereus* flower from late March to early June, although the period varies according to the species range and ecological conditions (Taylor, 1985). In general, the flowers begin to open early in the morning, e.g., 8:30 to 9:00 in *Echinocereus fasciculatus* (Grant and Grant, 1979a); 9:30 to 10:00 in the *E. enneacanthus* complex (Breckenridge and Miller, 1982) and E. *engelmannii* (Cota, pers. obs.). Flowers are completely open within the next two hours (9:00–11:00) and last three to four days, closing at night and under cloudy conditions (Taylor, 1985; Breckenridge and Miller, 1982). In most *Echinocereus* species, flowers are not fragrant; if scented, the fragrance is not strong.

The flowers of *Echinocereus* are funnelform and somewhat cup-shaped with numerous, colorful tepals. Nectaries are located below the attachment of the stamens. Herkogamy is the usual condition (the stamens are numerous and the anthers positioned below the stigma), hence they are spatially isolated. Protandry (centrifugal maturation of stamens) has been observed in flowers of the Echinocereus enneacanthus complex (Breckenridge and Miller, 1982), and in varieties engelmannii and munzii of E. engelmannii (Cota, pers. obs.). Therefore, dehiscence of anthers occurs before the stigma becomes receptive. When the stigma becomes receptive, the stigma lobes spread and provide a landing platform for potential pollinators. The stigmatic lobes are usually green and have a papillose texture. The papillae exude a sugary secretion that acts to adhere the pollen grains to the stigmatic surface (Bravo, 1978). Insects, mostly bees, land on the stigma and inadvertently deposit the pollen collected from the previous flower onto the stigmatic surface. They move to the stamens and crawl over the filaments and anthers, covering their bodies with pollen while feeding. They then move to another flower, and so promote pollen transfer. The same pattern has been documented for the E. enneacanthus complex (Breckenridge and Miller, 1982), and other cactus species, such as Opuntia spp. and Ferocactus wislizenii (Grant and Grant, 1979a, 1979b).

According to Taylor (1985), flowers of Echinocereus species seem to be self-incompatible and pollen from a genetically different plant is required in order to produce seed. Thus a self-incompatibility system appears to be common in the genus, and is probably controlled by the sporophyte (Ganders, 1976). Documented, non-autogamous species of Echinocereus are those in the E. enneacanthus complex (Breckenridge and Miller, 1982), E. viridiflorus complex (Leuck and Miller, 1982), E. fasciculatus (Grant and Grant,

Table 1. Primary pollinator agents in species of Echinocereus

Taxon	Bee	Hummingbird	Source
E. engelmannii	Megachile gentilis Aschmeadiella opuntiae		Grant & Grant, 1979a
E. enneacanthus	Diadasia afflicta D. rinconsi Lasioglossum forbesii Paralictus sp. Dialictus sp.		Breckenridge and Miller, 1982
E. fasciculatus var. boyce-thompsoni	Ceratina nanula Evylaeus amicus Megachile gentilis M. casadae Apis mellifera		Grant & Grant, 1979a
E. fendleri E. stramineus	Agapostemon texanus Diadasia rinconsi D. afflicta Lasioglossum forbesii Paralictus sp. Dialictus sp.		Cockerell, 1900 Breckenridge and Miller, 1982
E. triglochidiatus		Selasphorus Archilochus unidentified	Brown & Brown, 1979 Grant & Grant, 1967
var. neomexicanus E. viridiflorus	Agapostemon texanus Halictidae	3	Cockerell, 1900 Leuck and Miller, 1982

1979a), and E. adustus, E. pentalophus, E. pulchellus, and E. reichenbachii (Taylor, 1976).

Within Echinocereus, only two pollination syndromes have been documented: bee and bird pollination (Grant and Grant, 1967, 1979a). A third syndrome — hawkmoth — is suspected to occur in the genus, although no evidence is yet available. Scogin (1985) notes that nectar composition of one Echinocereus species matches that observed in other hawkmoth pollinated flowers. In addition, Miller (1988) suggests that bats are part of the pollination syndrome of *Echinocere*us. Bat pollination has been documented in columnar cacti such as Carnegiea gigantea and Stenocereus (Lemairocereus) thurberi (Alcorn et al., 1961, 1962), but Taylor (1989) considers it highly unlikely that cheiropterophily occurs in Echinocereus as its flowers do not have the unpleasant odor characteristic of bat flowers. Furthermore, white and/or creamy flowers, distinctive of bat pollination, occur only in E. leucanthus, and some varieties of E. pectinatus and E. dasyacanthus, E. pulchellus and E. knippelianus (Taylor, 1985). Nevertheless, the flowers of these taxa have not been reported to remain open late at night. Therefore, if bat pollination occurs in the genus, it has to take place during the day, probably late in the afternoon as bat activity usually starts before dusk. Apparently, the flowers of *Echinocereus* are not highly species-specific for pollination, as more than one species of bee or bird may pollinate different species. Table 1 lists the primary pollinator agents in Echinocereus flowers that have been reported in the literature.

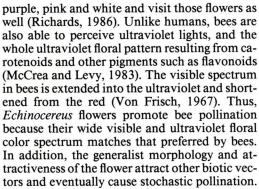
Bee Pollination Syndrome

Bee pollinated flowers of different sizes and colors occur in many of the species in the southwestern American cactus flora (Grant and Grant, 1979b), and are also common in most of the species of *Echinocereus*. These flowers are diurnal, open widely and have large, funnelform, bowl-shaped corollas with actinomorphic symmetry (Rowley, 1980; Grant and Grant, 1979a), e.g., E. laui (Fig. 1) and E. stramineus (Fig. 2). In general, the pollinator rewards, e.g., pollen and nectar, are usually abundant. However, studies of nectar amounts in some varieties of E. engelmannii indicated that at least in these bee pollinated taxa, nectar is not the primary reward as it was not detected (Cota, unpubl.). In addition, bee pollinated flowers of the E. viridiflorus complex produce minute amounts of nectar (Leuck and Miller, 1982). Therefore, abundance of pollen may compensate for the lack of nectar, and acts as a major reward. For most species, bee flowers are variously colored, although yellow is preferred, a pattern that matches the wide variation of color in cactus bee flowers.

Bee pollination is an effective mechanism for pollen transfer because bees do not require highly specific floral syndromes. The generalist or unspecialized open flower of *Echinocereus* is a clear example in most of its species. Furthermore, bees have a wide visual spectrum allowing them to distinguish and visit flowers of different colors. Yellow and blue flowers in the human visual spectrum are most typically visited by these insects, although bees are also able to distinguish



Fig. 1. Bee pollinated flower of *E. laui*, HBG 46456 (Photo: J. Trager).



Halictid bees are the most common visitors in the flowers of the *Echinocereus viridiflorus* and *E. enneacanthus* complexes, and they do not exhibit selective behavior in choosing species or flowers in sympatric populations (Leuck and Miller, 1982; Breckenridge and Miller, 1982). Also there was no preference observed for a particular color, floral shape, or anatomical structure.

Hummingbird Pollination Syndrome

The floral syndrome indicative of hummingbird pollination is characterized by usually medium to small size, non-scented diurnal flowers, with relatively short, reddish perianth-segments,



Fig. 2. Bee pollinated flower of *E. stramineus* (Photo: H. Cota).

a long receptacle-tube, and an elongated nectar chamber; pollen and nectar are generally abundant and rich in carbohydrates. For instance, the nectar of the flowers of Echinocereus coccineus contain concentrations about 32% sucrose (Parfitt, pers. comm.). The petals or perianth-segments tend to be short and oblique, giving more or less zygomorphic symmetry to the flower (Taylor, 1985), facilitating bird pollination (Rowley, 1980). The colors of the perianth range from bright red or scarlet to orange; however, flowers of other colors are also visited by hummingbirds. Pollination takes place when a hummingbird in search of nectar introduces its beak into the flower and makes contact with the stamens, simultaneously depositing pollen collected from the previous flower on the stigmatic surface, as has been observed in Echinocereus triglochidiatus (Fig. 3) (Grant and Grant, 1967).

In ornithophilous species, the effectiveness of pollination is related to the reciprocity of coadaptation between floral and bird morphology. The floral morphology best adapted to hummingbird preferences is dependent upon several related features such as color of the flower, proportions of the corolla, and length of the floral tube relative to the beak (Grant, 1949). In hummingbird pollinated flowers of syntopic taxa (species occurring in the same area and habitats), there is a general convergence of shape and color in dif-



Fig. 3. Hummingbird pollinated flowers of E. triglochidiatus var. mojavensis (Photo: W. Wisura).

ferent genera and families, e.g., Echinocereus triglochidiatus, Ipomopsis aggregata (Polemoniaceae) and Castilleja integra (Scrophulariaceae) (Brown and Brown, 1979). These three taxa exhibit such similarities as having red flowers, tubular corollas, and general floral attributes re-



Fig. 4. Hummingbird pollinated tubular flower of E. *pensilis* (Photo: J. Trager).

lated to a common hummingbird pollinator form. It seems that within ornithophilous flowers in convergent taxa, character displacement and pollinator specificity are an exception. Thus, as in bee pollinated flowers, different species of hummingbirds pollinate flowers with similar morphological patterns that have converged, offering the same or similar pollen and/or nectar rewards (Brown and Brown, 1979), such as *E. triglochidiatus*, whose flowers are reported to be pollinated by two species of hummingbirds (Table 1).

Data gathered from the literature indicates that within the genus Echinocereus, bird pollination is uncommon and occurs in only 6.25% of the species. So far, from the 44 species of Echinocereus (sensu Taylor, 1985), only E. triglochidiatus, E. polyacanthus, and E. scheeri (Taylor, 1985; Grant and Grant, 1967) have been reported to be hummingbird pollinated (Table 1). All these taxa are grouped in Taylor's (1985) section Triglochidiatus. In these taxa, the occurrence of pink flowers and the semi-nocturnal habit of the flowers (flowers remain open at night), may be an argument to discard diurnal pollination; however, the lack of fragance seems to eliminate nocturnal pollination (Taylor, 1985). In addition to the species in section Triglochidiatus, E. pensilis (section Morangaya) is suspected to be hummingbird pollinated because the flower exhibits the bird pollination syndrome (Fig. 4).

Hummingbird pollinated taxa of *Echinocereus* are widely distributed in mountainous regions in northern Mexico and southwestern U.S., at elevations from 1,800 to 3,000 meters (Benson, 1982; Taylor, 1985).

Hawkmoth Pollination Syndrome

Hawkmoth pollination is undocumented in the genus. Scogin (1985) correlated the chemical

composition of the nectar of Echinocereus huitcholensis (now under the name E. polyacanthus [Taylor, 1985]) with that required by hawkmoths, and assumes moths as putative pollinators of this taxon. However, as discussed previously, E. polyacanthus (E. huitcholensis) has red diurnal flowers and is hummingbird pollinated. No additional data for hawkmoth-pollinated species of Echinocereus exist in the literature, thus the occurrence of moth pollination in the genus is uncertain.

In terms of floral characteristics within the genus, the only likely species to be hawkmoth pollinated is Echinocereus leucanthus (Fig. 5). To date, the floral biology of this species has not been studied in detail. This species has white flowers, possibly increasing the chances for moth pollination to occur; however, the floral tube is relatively short, and the flowers are not scented. Other species of Echinocereus with forms of white flowers occur in E. knippelianus, E. fendleri, E. grandis, and E. pulchellus. According to Grant and Grant (1979b) and Rowley (1980), the hawkmoth syndrome is characterized by white or whitish nocturnal flowers with long slender floral tubes containing nectar, and are intensely scented. In the Cactaceae, typical moth-pollinated flowers are those of some species of Echinopsis, Epiphyllum, Hylocereus, and Selenicereus.

In general, moth-pollinated cacti occur in tropical and subtropical areas of Central and South America (Bravo, 1978). In turn, *Echinocereus leucanthus* is known only from southwestern Sonora and northwestern Sinaloa in subtropical lowlands (Taylor, 1985).

Discussion

Several factors may account for the relatively large level of species diversity in the genus *Echinocereus*. Some of these factors are related to floral anatomy and phenology, pollinator behavior, geographical barriers, chromosomal rearrangements, and asexual reproduction.

Grant and Grant (1965) suggest that the evolution of pollination systems in the Polemoniaceae has involved adaptive changes from one biotic vector to another, e.g., bee pollination to long-tongued fly. In the Cactaceae, in particular within *Echinocereus*, bee pollination is probably the ancestral condition, from which humming-bird, and hawkmoth (still to be documented) pollination evolved at different times under different selective pressures. The pollination syndromes in *Echinocereus* have apparently evolved from a generalist or non-specific pollination system to highly specialized systems, in which bird and perhaps hawkmoth pollinated flowers are at the end of the spectrum.

Within *Opuntia*, there are no known bee species that have evolved an intrafloral relationship with a single species (Grant and Hurd, 1979). In *Echinocereus*, the broad funnelform flowers are



Fig. 5. Flower of *E. leucanthus*, HBG 30018; the putative pollinator is a hawkmoth (Photo: J. Trager).

probably an adaptation toward more efficient use of the biotic environment, in this case the bee fauna. Thus, the relative diversity of bee visitors to flowers of different species may be an indication that interspecific floral isolation in the genus is not the main factor in its evolution. However, the interspecific pollination of compatible species may be prevented by two means: 1) mechanical barriers related to floral mechanisms that limit the effectiveness of pollination, and 2) pollinator behavior, which limits the pollinator to flowers of a single species. Both mechanical and ethological isolation imply some degree of complexity in the flowers and pollinators. However, ethological barriers in *Echinocereus* are still undocumented.

Grant (1949) suggests that floral isolation mechanisms have played an important role in angiosperm divergence, and that in order for floral isolation mechanisms to operate, individuals must have diverse floral morphology. In *Echinocereus*, floral isolation mechanisms, e.g., protandry and herkogamy, are probably important in promoting reproductive isolation and thus speciation in the genus. Similarly, while the flowers of *Echinocereus* species do not exhibit significant morphological variability, they are actually phenologically isolated. All species do not bloom at the same time, although some species have overlapping blooming seasons, even in sympatric

populations. In the case of closely related simultaneously flowering sympatric species, pollinator specificity may be enough to maintain species integrity even in the absence of other isolating mechanisms.

In Echinocereus, Taylor's (1985) taxonomic sections seem to be well defined according to their geographical distribution. Thus, if ethological isolation takes place in sympatric populations, it can reinforce reproductive isolation initially established by prezygotic and/or postzygotic events, or even geographical barriers. Another possible explanation for the high degree of infraspecific variation in allopatric populations, and among individuals of the same population, is cross-pollination. Cross-pollination involves gene flow and therefore promotes genetic variability.

Given the generalist floral morphology in most Echinocereus species, and the apparent lack of mechanical barriers influencing reproductive isolation, there are other factors to be considered involving the mechanisms of speciation. These may include changes in chromosome number and structure, such as polyploidy and chromosomal rearrangements. Indeed, documented cases of polyploidy and reproductive isolation have been reported by Parfitt (1987) in the E. engelmannii complex. Also, Cota (1991) notes that species richness in the genus is accompanied by numerical changes in chromosomes (polyploidy), and that differences in chromosome size might indicate cryptic chromosomal rearrangements, such as translocations and inversions.

In conclusion, little is known regarding the reproductive biology of Echinocereus. Most studies presented thus far are related to classical taxonomy, and a few have approached the dynamic biological factors involved in the diversity of the genus. Despite the lack of complete information, some assumptions can be made with respect to the evolution of the genus *Echinocereus*. The factors involved in the process of speciation of the genus are: 1) floral anatomy and phenology, including flowering season, time of opening, herkogamy and protandry; 2) chromosomal changes, both in structure (translocations and inversions) and in number (polyploidy); 3) geography; and 4) facultative asexual reproduction. These factors, independently or in conjunction, have been important in the establishment of reproductive isolating barriers leading to species diversity in the genus.

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BULBINE STUDY GROUP

Bulbines are short or stemless plants with fleshy leaves, an often tuberous caudex, and usually yellow flowers. The genus *Bulbine* is a member of the Asphodelaceae, a South African family with such genera of succulents as *Aloe, Haworthia* and *Gasteria*. Cultivating bulbines is more difficult because the tuberous species require a long dry rest in summer; otherwise, death by overwatering is common. In this respect they behave like mesembs, which come from many of the same areas. Generally not widely cultivated except for a few species, bulbines deserve more attention. Those interested in sharing their interest in *Bulbine* are invited to contact Lawrence M. Loucka, 335 Commonwealth Ave., New Britain, CT 06053-2403, USA, for a literature reference list and details on studies and experiences growing these plants.

CALL FOR SLIDES ON COLLECTIONS

One of the most popular programs at the 1991 convention in San Antonio was one by Seymour Linden on "Some collectors and their collections." It was composed of slides showing the growing facilities and favorite plants of various collectors, several of whom were present and discussed their collection. We will repeat this program during the 1993 convention in San Francisco. It will be presented by Dr. David Tufenkian, an enthusuastic grower from southern California.

So start right now selecting slides (or making new ones) of your greenhouses, shelters, growing arrangements or techniques, as well as your favorite plants. Selection will be made on the basis of

general appeal, not on the size of collection or specimens,

Please send your slides, accompanied by notes about you and your collection, to David Tufenkian, 1207 Dominion Ave., Pasadena, CA 91104 (818 794-3082). Send no more than 20 slides and be sure they get there by April 1, 1993.

DAVE GRIGSBY

Friends of Dave Grigsby, nurseryman and CSSA Fellow, will want to know that he is in a long-term-care nursing facility, suffering from the increasingly debilitating effects of Alzheimer's disease. Grigsby Cactus Gardens in Vista, Calif., continues under the management of Madelyn Lee and is able to maintain the support of Dave and his wife, who is also receiving full nursing care. Madelyn has been assuming increasing responsibilities for the management of the nursery for the last several years. As a trustee for the Grigsby family, Madelyn is able to continue the operation of the nursery. They offer the same high quality cacti and succulents that have made it world famous for over 30 years. Any correspondence for Dave can be addressed to the nursery and will be delivered by Madelyn.