INSECT POLLINATORS OF 12 MILKWEED (*ASCLEPIAS*) SPECIES

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Abstract. More than 1750 insects, collected on 12 species of *Asclepias*, were examined for the number of pollinial sacs extracted from donor flowers and for pollinial attachment to appendage and body hairs. The number of pollinial sacs missing from the translator arms of these pollinia was also determined and presumed to represent the number of pollinial sacs inserted into recipient flowers during pollination. These two figures (the number of pollinial sacs extracted and the number of pollinial sacs inserted) was used to rate the pollinating efficiency of an insect pollinator. The most important pollinators, such as the exotic honey bee (*Apis mellifera*), bumblebees (*Bombus*), large wasps (*Sphex, Tachytes, Myzinum*, and *Polistes*), and large butterflies (*Papilio*), not only carried relatively large numbers of pollinial sacs extracted from donor flowers, but apparently inserted large numbers of pollinial sacs into the stigmatic chambers of recipient flowers. Some milkweeds, such as, *A. hirtella* and *A. viridiflora*, were pollinated by bumblebees, while others, such as, *A. incarnata* and *A. verticillata*, were pollinated by a variety of bees, wasps, and butterflies. It is possible that the colonial mining bee (*Anthophora abrupta*) and other relatively large anthophorid bees (*Ceratina, Epeolus, Florilegus, Melissodes, Peponapis, Tetralonia, Triepoeolus*, and *Xenoglossa*), may have been the major pollinators of many milkweed species in pre-settlement times, but today have been replaced by the exotic honey bee (*Apis mellifera*).

INTRODUCTION

It has been two-hundred years since Sprengel (1793) suggested that insects were important in the removal of pollinia from flowers of *Asclepias*. Brown (1831) was the first to discover how pollination was accomplished in *Asclepias* and to conclude that insect vectors were absolutely necessary in the pollination of their flowers.

Because of the unusual morphology of milkweed flowers, their pollination by insect vectors is much more complex than is usually found in most other types of flowers. In order to better understand the insects that have evolved to pollinate them, it is important to understand the morphology of these flowers, the morphology of the pollium, and the mechanism of pollination.

Morphology of Milkweed Flowers

In *Asclepias*, the flowers are arranged in rounded or flat clusters called umbels. Depending on the species, these umbels in turn are arranged either at the tip of the stem (terminal) or along its sides (lateral). The central part of each flower consists of a short five-sided column containing five fused

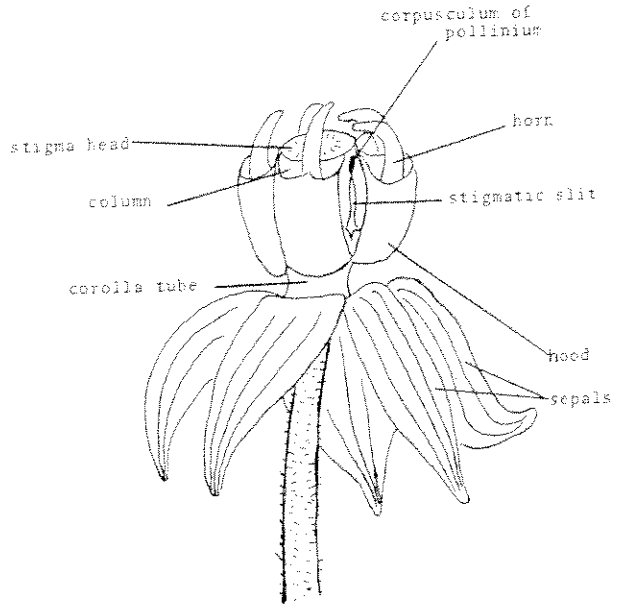

Figure 1. Flower of poke milkweed (*Asclepias exaltata*)

male filaments surrounding two female pistils and topped by a fleshy stigma head (or style table) (Figure 1). This column in turn is encircled by the most conspicuous and colorful part of the flower (corolla), consisting of 5 nectar-containing hoods. These hoods are composed of united petals, each with (or without depending on the species) an incurved horn. This corolla in turn is surrounded by 5 deflexed usually brightly-colored sepals. Stigmatic slits, bordered by two parallel corneous anther wings, are found on each of the five sides of the column between the five hoods. The opening between these anther wings leads into the stigmatic chamber (Corry 1883, Frye 1902, and Brookman 1981).

Morphology of the Pollinium (or Pollinarium)

Each stamen has two flattened pyriform pollinial sacs, each of which contains a waxy pollen mass of approximately 500 pollen grains (Figure 2). Each pollinial sac is attached to a translator arm (or retinacula) with a characteristic knee bend. The translator arms of two adjacent pollinial sacs of different anthers in turn are joined together to a blackish-brown oval corpusculum (or gland) with a dorsal medial slit. Two pollinial sacs, together with their translator arms and a central common corpusculum, constitutes a pollinium (or pollinarium). Only the corpusculum is visible on the outer surface of

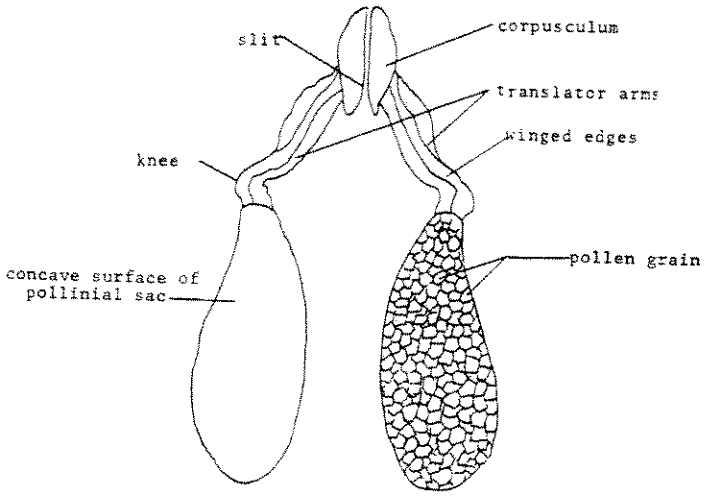

Figure 2. Pollinium of Sullivant's milkweed (*Ascelepias sullivantii*)

the column at the upper end of the stigmatic slit, while the remainder of the pollinium (translator arms and pollinial sacs) are hidden within the column. Therefore, in each flower, there are 5 corpuscula which are visible on each of the 5 sides of the column, and 10 pollen sacs which are hidden in each column (Brookman 1981).

Pollination of Milkweed Flowers

The pollination of *Asclepias* flowers involves two separate steps: (1) the extraction of a pollinium with its two pollinial sacs from a donor flower and (2) the insertion of one of the these pollinial sacs into a stigmatic chamber of a recipient flower. The first step is accomplished in the following manner. As the insect pollinator feeds on the nectar in the hoods of a donor flower, a leg may be guided upward by the two parallel anther wings of a stigmatic slit toward a projecting corpusculum. With further movement upward, a bristle or hair may wedge in the fine dorsal slit in the corpusculum of the pollinium which may then be pulled out (or extracted) from the column. When first extracted the pollinial sacs have

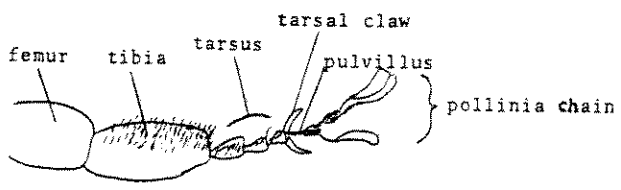

Figure 3. Hind leg of honey bee (*Apis mellifera*) with attached pollinal chain.

their flat sides lying perpendicular to the stigmatic slit and cannot be inserted into the stigmatic chamber of a receptor flower in this position.

The second stage of pollination begins with the drying of the withdrawn pollinium's translator arms while attached to the pollinator's appendage or body hairs. This causes the pollinia to turn inward 90 degrees and results in the concave surface of these pollinial sacs to face downward. The pollinial sacs in this position are now in the same plane as that of a stigmatic slit and can now be inserted into a stigmatic chamber of a recipient flower. The same leg movements that were responsible for the removal of the pollinium from the donor flower causes the leg to be guided upward along the stigmatic slit of a recipient flower. The corpusculum, attached to the pollinator's hair, does not enter the stigmatic slit of the recipient flower, but slides over its anther wings. The first part of the pollinium to enter the stigmatic chamber is the right-angled bend in the translator arm (knee bend), followed by the remainder of the translator arm with the pollinial sac following behind. The pollinial sac with its translator arm is moved upward inside the stigmatic chamber, eventually reaching the superior end of the stigmatic slit. Following the wedging of the pollinial sac in the stigmatic chamber, the further upward movement of the pollinator's leg causes the translator arm to break off. This leaves the pollinial sac in the stigmatic chamber (Robertson 1886, Betz personal observations).

Chain formation may result immediately after the insertion of a pollinial sac into the stigmatic chamber by the continued upward movement of the pollinator's leg. The broken remainder of the translator arm is directed toward the projecting corpusculum at the top of the stigmatic slit, and this flattened broken translator arm wedges into the dorsal slit of the corpusculum. Thus, with the continued upward movement of the leg, a new pollinium is extracted from the flower, producing a chain or cluster of three pollinial sacs. The recipient flower now has become a donor flower. Broken and intact translator arms of chains and clusters of pollinia can act as new attachment sites for other pollinia, forming all sorts of straight and branching chains of pollinia. It is probable that these pollinial chains also increase the likelihood of the insertion of a pollinial sac into a stigmatic chamber of a receptor flower as compared to the situation in which a single pollinium is attached to a body or appendage hair.

Many of the insects found on *Asclepias* flowers are not pollinators of those flowers. Some insects (visitors) visit the flowers to suck nectar, but they almost never extract pollinia. These are recognized as non-pollinators and are sometimes designated as "nectar thieves" (Willson et al. 1979). Others (pollen extractors) may extract pollinia from donor flowers, but they almost never insert a pollinial sac into a recipient

flower. The pollen inserters (or actual pollinators) of *Asclepias* flowers are those insects that complete both of the two important processes of pollination: (1) the extraction of two pollinial sacs from a donor flower; and (2) the insertion of at least one of these pollinial sacs into the stigmatic chamber of a recipient flower. In all studies these latter two groups (pollen extractors and pollen inserters) are lumped together into "pollen vectors".

In Europe insect species collected on the flowers of *Asclepias syriaca*, an introduced species, were compiled by Delpino (1867), Hildebrand (1866), and Mueller (1873, 1882). No distinctions were made as to which ones were visitors, pollen extractors, or pollen inserters.

In North America, most studies carried out on the insect visitors of *Asclepias* distinguished between visitors and those observed carrying pollinia (pollen extractors), but did not differentiate between pollen extractors and pollen inserters. Robertson (1886, 1887a, 1887b, 1891, 1895, and 1929) carried out extensive studies on the insect visitors to the flowers of eight North American *Asclepias* species found in southwestern Illinois (*A. hirtella, A. incarnata, A. purpurascens, A. sullivantii, A. syriaca, A. tuberosa, A. verticillata,* and *A. viridiflora*). He distinguished between those that were pollinia extractors and those that were not (visitors). Macior (1965) studied the bees and wasps carrying pollinia of three species in southeastern Wisconsin (*A. incarnata, A. syriaca,* and *A. verticillata*). He recorded the frequency and location of the corpuscula on various parts of the body and distinguished between those attached directly to body parts (basal) or in chains to translator arms of other corpuscula (distal). Frost (1965) studied the insect visitors to three species of milkweeds in Pennsylvania (*A. incarnata, A. syriaca,* and *A. tuberosa*) and recorded the number and attachment of the pollinia carried on various body parts (mouth, claws, pulvilli, tibiae, and tarsi). Willson et al. (1979) in central Illinois recorded the insect visitors to *A. verticillata*. They listed those species that were carrying pollinia and reported the average number of pollinia carried. Willson and Bertin (1979) in central Illinois listed the insect visitors to *A. syriaca* and also identified those species carrying pollinia along with the average number of pollinia being carried.

Thus, in the absence of definitive information, this present study was primarily undertaken to distinguish the pollen inserters from the pollen extractors of *Asclepias* flowers. In addition, the points of attachment of the pollinia to the body hairs and appendages of the pollinators were also determined in order to record similarities and differences among insect species carrying pollinia from the same or different species of *Asclepias*.

Due to the relatively low extraction and insertion of pollinial sacs into *Asclepias* flowers by many native insects compared to that of the exotic honey bee (*Apis mellifera*), speculations are made concerning the pre-settlement pollinators of *Asclepias* flowers.

METHODS

Studies on the insect pollinators of 12 species of *Asclepias* were extensively carried out between 1965 and 1971 and were continued sporadically for another 20 years on five of the rarer species (*A. amplexicaulis, A. hirtella, A. lanuginosa, A. meadii,* and *A. viridiflora*). Insects were collected from more than 40,000 milkweed plants, 93.8% of which belonged to three common species (*A. incarnata, A. syriaca,* and *A. verticillata*). Most of the populations studied were in northeastern Illinois and northwestern Indiana. In addition, some studies were done on populations of *A. exaltata* in the Devil's Lake area of central Wisconsin. Most of the data for *A. meadii* were gathered from plants growing in western Missouri and northeastern Kansas.

Some of the milkweed species grew in large colonies with thousands of plants (ramets) as was the case with *A. incarnata, A. syriaca,* and *A. verticillata*. Whereas others, such as *A. lanuginosa*, formed smaller clones consisting only of hundreds of plants. Other species, such as *A. sullivantii*, grew in isolated populations consisting of a half-dozen plants. Still others, such as *A. hirtella, A. meadii* and *A. viridiflora*, grew as isolated plants (genets) or small clusters of two or three plants.

Populations of *Asclepias* were visited throughout the blooming season which usually lasted about two or three weeks depending on the species. Insects were collected from flowers by netting two to four times per week for periods of one to five hours at variable times throughout the day. A few attempts to collect insects nocturnally from some milkweeds were made, but no insects were taken. Insect specimens were brought back to the laboratory, pinned, and, in most cases, identified to species. Corroborating identifications were also made through the use of the insect collections at the Field Museum of Natural History, Chicago, Illinois.

The identified insects were checked under a dissecting microscope for the number of corpuscula they carried, as well as for the points of attachment of the corpuscula to the body or appendage hairs and bristles. In addition, the number of pollinial sacs still attached to the translator arms (i.e., whether 0, 1, or 2 sacs) was recorded.

The number of pollinial sacs extracted from a donor flower by a pollinating insect was determined by first noting the number of corpuscula attached directly to the body hairs and

Table 1. Percentage of Presumed Pollen Sac Insertion in *Asclepias*.

Milkweed Species & Insect Vector (#) = sample size	# Pollinial Sacs Extracted by Species from Donor Flowers of	% Pol.Sacs Inserted into Recipient Flowers of	Mean # Pol. Sacs Extracted for Insect Species on
A. amplexicaulis			
Apis mellifera (1)	0	00.0	00.0
Megachile brevis (3)	0	00.0	00.0
A. exaltata			
Apis mellifera (6)	62	85.5	10.3
Bombus pennsylvanicus (18)	54	88.9	3.0
Ancyloxipha numitor (2)	4	25.0	2.0
Epargyreus clarus (3)	2	0.0	0.7
Lasius niger (50)	4	25.0	0.1
A. hirtella			
Bombus affinis (2)	182	51.6	91.0
Bombus griseocollis (2)	64	38.0	32.0
A. incarnata			
Apis mellifera (23)	2068	74.2	89.9
Bombus griseocollis (32)	1484	80.4	46.4
Bombus nevadensis auricom(6)	564	72.5	94.0
Papilio sp. (7)	384	75.0	54.9
Sphex ichneumoneus (26)	1904	79.4	73.2
Sphex pennsylvanicus (14)	1794	75.8	128.1
Colias philodice (4)	46	71.8	11.5
Danaus plexipus (5)	66	75.8	13.2
Limenitis archippus (6)	98	64.3	16.3
Megachile latimonas (3)	48	25.0	16.0
Pieris rapae (4)	24	58.3	6.0
A. lanuginosa			
Colletes armatus (1)	8	37.5	8.0
Megachile mendica (1)	0	0.0	0.0
A. meadii			
Anthophora abrupta (6)	26	42.3	4.3
Apis mellifera (1)	0	0.0	0.0
Bombus affinis (1)	4	0.0	4.0
Bombus griseocollis (1)	2	0.0	2.0
A. purpurascens			
Apis mellifera (30)	480	83.3	16.0
Bombus pennsylvanicus (6)	12	58.3	2.0
A. sullivantii			
Apis mellifera (120)	1428	77.9	11.9
Bombus fervidus (7)	42	90.5	6.0
Bombus pennsylvanicus (20)	160	86.9	8.0
Sphex ichneumoneus (1)	18	83.3	18.0

Table 1, continued.

Milkweed Species & Insect Vector (#) = sample size	# Pollinial Sacs Extracted by Species from Donor Flowers of	% Pol.Sacs Inserted into Recipient Flowers of	Mean # Pol. Sacs Extracted for Insect Species on
A. syriaca			
Apis mellifera (275)	7776	60.9	28.3
Bombus pennsylvanicus (865)	4	0.0	0.0
Sphex ichneumoneus (1)	4	75.0	4.0
A. tuberosa			
Apis mellifera (69)	1138	71.5	16.5
Bombus pennsylvanicus (14)	24	50.0	2.0
Sphex ichneumoneus (2)	218	83.5	109.0
Colletes armatus (7)	8	75.0	1.1
Danaus plexippus (6)	2	50.0	0.3
Lygaeus kalmii (25)	2	0.0	0.1
Mechachile brevis (20)	10	70.0	0.5
Strymon titus (6)	8	0.0	1.3
A. verticillata			
Apis mellifera (12)	342	32.2	28.5
Bombus griseocollis (7)	230	64.8	32.9
Myzinum quinquecintum (15)	654	52.1	43.4
Polistes fuscatus (2)	298	33.6	149.0
Prionyx atratus (2)	34	35.6	17.0
Sphex ichneumoneus (11)	114	60.5	10.4
Sphex pennsylvanicus (12)	424	53.3	35.3
Tachytes mandibularis (4)	40	30.0	10.0
Colletes compactus (2)	84	10.7	42.0
Ceratogastra ornata (2)	16	25.0	32.0
Epibembex nubilipennis (2)	4	50.0	2.0
Megachile latimanus (1)	4	75.0	4.0
A. viridiflora			
Bombus griseocollis (5)	176	39.8	35.2

in the pollinial chains. Since each corpusculum has two pollinial sacs attached to it, the total number of pollinial sacs extracted by a pollinating insect from donor flowers is double the number of corpuscula. However, more pollinia may have been extracted, but have been lost. This can occur by accidental breakage of a chain or by being brushed off by an insect cleaning itself. Thus, the actual number of pollinia extracted may be more. For this reason, this calculated number of extracted pollinial sacs is a presumed number. Table 1 shows the total number of extracted pollinial sacs for each insect species observed in this study.

The number of pollinial sacs inserted into a recipient flower by a pollinating insect was determined by subtracting the number of pollinial sacs still attached to translator arms from the total number of pollinial sacs calculated to have been extracted from donor flowers. Since some pollinial sacs may have been accidentally lost for reasons other than being used in pollination, the number of inserted pollinial sacs actually may have been different from the computed one. Thus, the number of inserted pollinial sacs computed is a presumed number.

Using these data, the total number of pollinial sacs inserted into the stigmatic chambers of recipient flowers was con-

Table 2. Insect Pollinators of *Asclepias* and the Species Pollinated.

Species	Family	Milkweed Pollinated
HYMENOPTERA		
Bees		
Anthophora abrupta (digger bee)	Anthophoridae	*A. meadii.*
Apis mellifera (honey bee)	Apidae	*A. amplexicaulis* *A. exaltata* *A. incarnata* *A. meadii* *A. purpurascens* *A. sullivantii* *A. syriaca* *A. tuberosa* *A. verticillata*
Bombus affinis (bumble bee)	Apidae	*A. affinis* *A. meadii*
Bombus fervidus (bumblebee)	Apidae	*A.sullivantii*
Bombus griseocollis (prairie bumblebee)	Apidae	*A. hirtella* *A. incarnata* *A. meadii* *A. verticillata* *A. viridiflora*
Bombus nevadensis auricomus (bumblebee)	Apidae	*A. incarnata*
Bombus pennsylvanicus (bumblebee)	Apidae	*A. exaltata* *A. purpurascens* *A. sullivantii*
Colletes armatus (plasterer bee)	Colletidae	*A. lanuginosa* *A. tuberosa*
Colletes compatus (plasterer bee)	Colletidae	*A. verticillata*
Megachile brevis (leafcutting bee)	Megachilidae	*A. tuberosa*
Megachile latimanus (leafcutting bee)	Megachilidae	*A. incarnata* *A. verticillata*
Megachile mendica (leafcutting bee)	Megachilidae	*A. lanuginosa*
Wasps		
Ceratogastra ornata (ichneumonfly)	Ichneneumonidae	*A. verticillata*
Epibembix nubilipennis	Sphecidae	*A. verticillata*
Myzinum quinquecintum (five-banded tiphiid wasp)	Tiphiidae	*A. verticillata*
Polistes fuscatus (northern paper wasp)	Vespidae	*A. verticillata*
Prionyx atratus (thread-waisted wasp)	Sphecidae	*A. verticillata*

Table 2, continued.

Species	Family	Milkweed Pollinated
Sphex ichneumoneus (great golden thread-waisted wasp)	Sphecidae	*A. incarnata* *A. sullivantii* *A. tuberosus* *A. verticillata*
Sphex pennsylvanicus (great black thread-waisted wasp)	Sphecidae	*A. incarnata* *A. verticillata*
Tachytes mandibularis (thread-waisted wasp)	Sphecidae	*A. verticillata*
Lepidoptera/Butterflies		
Ancyloxipha numitor (least skipper)	Hesperiidae	*A. exaltata*
Colias philodicee (common sulfur butterfly)	Pieridae	*A. incarnata*
Danaus plexippus (monarch butterfly)	Danaidaee	*A. incarnata* *A. tuberosa*
Epargyreus clarus (silver spotted skipper)	Hesperiidae	*A. exaltata*
Limenitis archippus (viceroy)	Nymphalidae	*A. incarnata*
Papilio polyxenes (black swallowtail)	Papilionidae	*A. incarnata*
Pieris rapae (cabbage butterfly)	Pieridae	*A. incarnata*
Strymon titus (coral hairstreak)	Lycaenidae	*A. tuberosa*

verted into a percentage of the total number of pollinial sacs extracted from donor flowers (Table 1).

The mean number of pollinial sacs extracted was calculated for the sample population of each insect species found in association with a particular *Asclepias* species. This mean was used as a measure of the ability of a species to extract pollinial sacs from donor flowers (Table 1).

Even though the percentages and means as calculated above are based on presumed numbers, it is felt that these derived data are still useful for comparative purposes. They provide a basis for understanding the relative effectiveness of the various insects observed in this study as pollinators for the different species of milkweeds.

RESULTS

One thousand seven hundred and fifty two insect specimens, representing 28 species and belonging to 10 different families, were collected and reported in this study (Tables 1 and 2). Three groups, the larger bees, wasps, and butterflies were the most important groups in pollinating *Asclepias* flowers. These groups of insects were important because they extracted large numbers of pollinial sacs from donor flowers, and inserted a high percentage of these pollinial sacs into the stigmatic chambers of recipient flowers. The two most important families of bees were the *Apidae*: honey bees (*Apis*) and bumble bees (*Bombus*), and the *Anthophoridae*: mining bees (*Anthophora*). Among the important families of wasps, were the *Sphecidae*: thread-waisted wasps (*Sphex, Prionyx*, and *Tachytes*); *Vespidae*: paper wasps (*Vespa*); and the *Tiphiidae* (*Myzinum*). Important butterflies include the *Papilionaceae*: swallowtails (*Papilio*) and *Nymphalidae* (brushfooted butterflies). *Apidae, Sphecidae*, and *Papilionaceae* were the only families pollinating *A. exaltata* (poke milkweed), *A. hirtella* (tall green milkweed), *A. meadii* (Mead's milkweed), *A. purpurascens* (purple milkweed), *A. sullivantii* (Sullivant's milkweed), and *A. viridiflora* (short green milkweed). For most of the other milkweeds this group of three families constituted at least 90% of the pollinators. For example, in *A. incarnata* (marsh milkweed) this group accounted for 97.3% of the pollination as well as 98.8% in *A. tuberosa* (butterfly weed) and 98.2% in *A. verticillata* (whorled milkweed).

Table 3. Attachment of Pollinia to appendages of *Bombus sp.* **pollinating** *Asclepias viridiflora, A. hirtella* **and** *A. exaltata.*

Insect Appendage	*B.griseocollis* (*A. viridiflora*) (5)		*B.affinis* (*A. hirtella*) (2)		*B.griseocollis* (*A. hirtella*) (2)		*B. pennsylvanicus* (*A. exaltata*) (18)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	2	1	0	0	6	3	6	3
Claws								
front	0	0	0	0	0	0	0	0
middle	0	0	0	0	0	0	0	0
hind	0	0	0	0	0	0	0	0
Pulvilli								
front	0	0	0	0	0	0	0	0
middle	0	0	0	0	0	0	0	0
hind	0	0	0	0	0	0	0	0
Tarsi								
front	24	16	18	13	2	1	16	16
middle	76	38	16	9	0	0	18	17
hind	56	14	10	10	0	0	14	12
Tibiae								
front	2	0	16	8	4	1	0	0
middle	16	1	24	10	20	14	0	0
hind	0	0	56	28	4	0	0	0
Femur								
front	0	0	0	0	0	0	0	0
middle	0	0	4	1	4	1	0	0
hind	0	0	10	4	0	0	0	0
Trochanter								
front	0	0	0	0	0	0	0	0
middle	0	0	10	5	12	1	0	0
hind	0	0	4	2	0	0	0	0
Coxa								
front	0	0	2	0	0	0	0	0
middle	0	0	2	0	8	2	0	0
hind	0	0	0	0	0	0	0	0
Thorax	0	0	8	4	4	0	0	0
Abdomen	0	0	2	0	0	0	0	0
Total	176	70	182	94	64	23	54	48
% Transfer	(39.8)		(51.6)		(38.0)		(88.8)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

Table 4. Attachment of Pollinia to body parts of *Apis mellifera* pollinating different species of *Asclepias*

	A. purpurascens (30)		*A.sullivantii* (120)		*A.incarnata* (23)		*A.tuberosa* (69)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	0	0	70	10	98	63	0	0
Claws								
front	6	5	194	134	180	144	20	14
middle	2	2	322	265	194	149	84	67
hind	2	2	336	277	142	122	96	83
Pulvilli								
front	108	77	160	136	272	228	30	26
middle	158	142	206	171	184	155	94	74
hind	152	141	134	115	108	98	58	45
Tarsi								
front	4	1	0	0	222	151	70	39
middle	20	14	0	0	338	243	174	117
hind	28	16	0	0	268	171	172	118
Tibiae								
front	0	0	0	0	0	0	8	2
middle	0	0	4	3	0	0	22	17
hind	0	0	2	1	52	3	310	212
Totals	480	400	1428	1112	2058	1527	1138	814
%Transfer	(83.3)		(77.9)		(74.2)		(71.5)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

Families of lesser importance for pollination were the leaf-cutting bees *Megachilidae*: (*Megachile*); plasterer bees *Colletidae* (*Colletes*); *Ichneumonidae*: ichneumon wasps (*Ceratogastra*); *Danaidae*: monarch butterflies (*Danaus plexipus*); *Hesperiidae* skippers (*Ancyloxipha*); *Nymphalidae*: viceroys (*Limenitis*) and *Pieridae*: sulfurs (*Pieris*). (Table 1 and 2).

Many insects, such as the cerambycid milkweed beetles (*Tetraopes tetraophthalmus* and *T.femoratus*), are commonly found on milkweed flowers but they are usually not pollinators (Robertson 1927 and Betz personal observations). In addition, the monarch butterfly (*Danaus plexippus*), a common visitor to *Asclepias* flowers, appears to be a minor pollinator in only two species (*A. incarnata* and *A. tuberosa*), in that it extracts and inserts relatively few pollinial sacs.

Pollination Characteristics

Points of Corpuscula Attachment.

The point of attachment of the corpusculum and pollinia to the body and appendage hairs, and to the bristles of an specimen varied depending on the insect species and the *Asclepias* species being pollinated (Tables 3, 4, 5, and 6). Most of the pollinia were attached to the lower parts of the appendages, i.e., the hairs on the tarsi and tibia, pulvilli bristles, and claws (Figure 3). Very few were attached to the mouth (palpi and tongue). In a special case involving the bumble bees (*Bombus griseocollis* and *B.affinis*) found on the tall green milkweed (*A. hirtella*), the pollinia were not only attached to hairs and bristles of lower leg appendages, but also further up on the leg and closer to the body, i.e., femur, trochanter and coxa. Some were even on the thorax and abdomen (Table 3). This may be due in part to the fact that the umbels of small flowers in *A. hirtella* are loose with relatively long and thin pedicels. It is possible that when sucking nectar the bumble bee sinks down into the mass of flowers and extracts pollinia using hairs and bristles closer to its body.

Number of Pollinial Sacs,Extracted.

The mean number of pollinial sacs extracted from donor flowers by a pollinating species varied, depending on both

the insect species and the species of *Asclepias* (Table 1). The insect species extracting the highest number of pollinial sacs was the paper wasp (*Polistes fuscatus*). They were collected from *A. verticillata* and had a mean of 149.0 extracted pollinial sacs. The great black thread-waisted wasp (*Sphex pennylvanicus*) found on *A. incarnata* had a mean of 128.1. In contrast, the great golden thread-waisted wasp (*Sphex ichneumoneus* found on *A. verticillata* extracted only a mean of 10.4 pollinial sacs. The monarch butterfly (*Danaus plexippus*) collected from *A. tuberosa* had only a mean of 0.3 pollinial sacs.

The number of pollinial sacs extracted by specimens within a species varied widely. Of the two specimens of *B. griseocollis* collected on *A. hirtella*, one carried 40 pollinial sacs, while the other carried 24. Of ten specimens of honey bee (*Apis mellifera*) collected on *A. syriaca*, one carried 92 pollinial sacs, and second 50, a third 4, six specimens carried 2, and one specimen none at all.

Percent Insertion of Pollinial Sacs.

The highest percentages of pollinial sacs inserted by a species was found among the bumble bees (*Bombus*). The black-banded bumble bee (*B. fervidus*) inserted 90.5% of the pollinial sacs in the pollination of *A. sullivantii*. *Bombus pennsylvanicus* inserted 88.9% of the pollinial sacs in the pollination of *A. exaltata* (Table 1).

Pollinators by Plant Species

Asclepias amplexicaulis (sand milkweed). Observations on 178 flowering stems of this milkweed during two growing seasons resulted in the collection of only two species of insects: one honey bee (*Apis mellifera*) and three (two males and one female) leaf-cutting bees (*Megachile brevis*) (Table 1). None of the four specimens had extracted pollinial sacs. Thus it is unlikely that these were major pollinators of this milkweed species. Further studies need to be undertaken on this species.

A. exaltata (poke milkweed). Observations made on 440 flowering stems of this milkweed during two growing seasons resulted in the collection of two species of insects which had extracted and inserted pollinial sacs (Table 1). Of the eighteen specimens of *Bombus pennsylvanicus* examined, 8 carried pollinial sacs principally on the tarsal hairs (Table 3). Eighty-nine percent of the extracted 54 pollinial sacs were inserted. Of the six honey bees (*Apis mellifera*) examined, two also carried pollinial sacs principally on the pulvilli. Eighty-six percent of the extracted 62 pollinial sacs were inserted.

Three specimens of silver spotted skipper (*Epargyreus clarus*) were collected, but only one carried two pollinial sacs. None of these was inserted. Two specimens of the least skipper (*Ancyloxipha numitor*) carried 4 pollinial sacs, and only one was inserted. In addition, many tiny Diptera and robber flies (*Erax rufilabris*) were seen to visit the flowers, but none carried pollinial sacs.

A. hirtella (tall green milkweed). Observations on 58 stems of this milkweed over two growing seasons resulted in the collection of only two species of bumble bees (Table 1). The two specimens of *B. affinis* inserted 51.6% of the 182 pollinial sacs they originally extracted. The two specimens of *B. griseocollis* collected had inserted 38.0% of the 64 pollinial sacs extracted from recipient flowers. Although the largest numbers of corpuscula in both of these species were attached to the hairs of the tibia and tarsi, substantial numbers were also attached to the hairs of the femur, trochanter, coxa, thorax, and abdomen.

A. incarnata (marsh or swamp milkweed). Observations on 10,500 stems of this milkweed over two blooming seasons indicated that large numbers of a variety of insects were attracted to the flowers of this species (Table 1). The 23 specimens of honey bee (*A. mellifera*) collected inserted 74.2% of the extracted 2068 pollinial sacs. Most of these pollinial sacs were carried on the claws, pulvilli, and tarsal hairs, but they were also carried to a lesser extent on the tibial hairs (Table 4). The 32 specimens of *B. griseocollis* collected inserted 80.4% (1193) of the extracted 1484 pollinial sacs. The 6 specimens of *B. nevadensis auricomis* inserted 72.5% (409) of 564 pollinial sacs extracted. Most of the corpuscula were attached to the tarsal hairs, but they were also attached to the claws, pulvilli and tibial hairs. The leaf-cutting bee *Megachile latimanus* appeared to be a minor pollinator of this milkweed (Table 1).

The 26 specimens of the golden thread-waist wasp (*Sphex ichneumoneus* collected from *A. incarnata* inserted 79.4% of the pollinial sacs of the extracted 1904 pollinial sacs, while the black thread-waist wasp (*S. pennsylvanicus*) inserted 75.8% of the extracted 1794 pollinial sacs. In both species most of the pollinial sacs were carried on the tarsal claws, but a substantial number were also carried on the mouth, claws, pulvilli and tibial hairs in both species (Table 5).

Among the butterflies collected, 6 specimens of the viceroy (*Limenitis archippus*) inserted 64.3% of the 98 extracted pollinial sacs, while the 5 specimens of the monarch (*Danaus plexippus*) inserted 75.8% of the 66 extracted pollinial sacs. The 7 specimens of the black swallowtail (*Papilio polyxenes*) inserted 75.0% of the 384 extracted pollinial sacs. Other species of butterflies collected included 6 specimens of the common sulfur (*Colias philodice*) and 4 specimens of the cabbage butterfly (*Pieris rapae*). Most of the corpuscula were attached to the tarsal hairs for all of these *Lepidoptera* (Table 6).

Table 5. Attachment of Pollinia to body parts of *Sphex sp.* wasps pollinating *Asclepias*.

	Sphex ichneumoneus (*A.incarnata*) (26)		*Sphex pennsylvanicus* (14)		*Sphex ichneumoneus* (*A.verticillata*) (11)		*Sphex pennsylvanicus* (12)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	48	27	12	11	0	0	0	0
Claws								
front	32	25	30	23	4	0	0	0
middle	8	6	2	1	2	1	0	0
hind	6	5	8	6	4	1	0	0
Pulvilli								
front	50	43	26	22	2	0	16	3
middle	16	14	4	3	8	5	0	0
hind	18	9	6	5	2	0	6	4
Tarsi								
front	874	707	810	604	62	46	278	140
middle	392	324	508	419	24	14	66	32
hind	414	321	370	257	6	2	58	37
Tibiae								
front	20	13	12	5	0	0	0	0
middle	16	10	2	1	0	0	0	0
hind	10	8	4	2	0	0	0	0
Totals	1904	1512	1794	1359	114	69	424	226
% Transferred	(79.4)		(75.8)		(60.5)		(53.3)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

A. lanuginosa (woolly milkweed). Observations on 255 flowering stems of this milkweed during two blooming seasons resulted in the collection of only two specimens (Table 1). One, a colletid bee (*Colletes armatus*), carried 8 pollinia on the tarsal hairs of the second and third pairs of legs. Three pollinia were incomplete and may have been inserted. The leaf-cutting bee (*Megachile mendica*), bore no pollinia (Table 1). Many tiny *Diptera* and wingless *Formicidae* (ants) were observed on the flowers, but none of the many examined had pollinial sacs attached. Several specimens of *Bombus griseocollis* were present in the vicinity of the blooming plants, but were not observed to visit the flowers or carry pollinial sacs.

A. meadii (Mead's milkweed). Few pollinators were observed on 140 flowering stems of this milkweed during nine blooming seasons. Two bumble bee queens (*B. affinis* and *B. griseocollis*) were collected, but were not found to have attached pollinia. Six specimens of the mining bee (*Anthophora abrupta*) were collected that had extracted 26 pollinial sacs, of which 11 (42.3%) had been inserted (Table 1). Ants (*Formicidae*) were commonly observed feeding on the nectar dripping from the nectaries, but they carried no pollinia.

A. purpurascens (purple milkweed). Observations made on 65 flowering stems of this milkweed during two blooming seasons resulted in the collection of 30 specimens of the exotic honey bee (*Apis mellifera*). This exotic bee species appears to be the major pollinator of this milkweed species. Six specimens carried 480 extracted pollinial sacs, of which 399 (83.1%) were inserted. Seven specimens of *Bombus pennsylvanicus* were also collected. Three of them extracted 12 pollinial sacs. Only 7 of these pollinial sacs (53.3%) were inserted (Table 1).

A. sullivantii (prairie milkweed). Observations on 575 flowering stems of this milkweed during two blooming seasons resulted in the collection 120 specimens of the exotic honey

bee (*Apis mellifera*). This insect far outnumbered the other insect species observed visiting this milkweed (Table 1). Out of 1428 extracted pollinial sacs 77.8% (1112) were missing and inserted. The pollinia (94.7%) were attached to the claws and pulvilli (Table 4).

In addition to honey bees, two species of bumble bees were collected on flowers of this plant. Twelve specimens of *Bombus pennsylvanicus* out of the 20 collected carried pollinia. Ninety-five percent of the 160 pollinial sacs extracted were on their claws. Of these, 86.9% (152) were inserted (Table 3). Seven specimens of *B. fervidus* were also collected on this milkweed, of which three were found to be carrying 42 pollinial sacs. In this species 90.5% (38) were inserted.

One specimen of the great golden thread-waisted wasp (*Sphex ichneumoneus*) was also collected on *A. sullivantii*. Of the 18 extracted pollinial sacs of this milkweed, 83.3% (15) were inserted. In addition, it also carried a large number of pollinia from the smaller marsh milkweed (*A. incarnata*) which grew nearby. It is interesting to note that some of the pollinia from *A. sullivanti* carried by this wasp were attached to ligaments (broken translator arms) of *A. incarnata*. These in turn were attached in chains to the relatively large pulvillus of this wasp.

At one site other species of wasps were seen visiting a colony of *A. incarnata* not more than 20 feet away from *A. sullivantii*, but many spot-checks on the kind of pollinia carried by these wasps showed that most did not visit the larger flowers of *A. sullivantii*. Those that did, did not pick up any pollinia.

Small *Diptera* and *Lasius niger*, a wingless ant, were also observed on flowers of *A. sullivantii*, but they were too small to be pollinators and carried no pollinia. Occasionally a monarch (*Danaus plexippus*) or cabbage butterfly (*Pieris rapae*) was seen to visit the blooms, but none was found to carry enough pollinia to be an effective pollinator.

A. syriaca (common milkweed). Observations on 12,000 flowering stems of this milkweed were carried out through two blooming seasons. The exotic *Apis mellifera* was by far the major pollinator of this milkweed. Almost all of the 275 specimens of *Apis mellifera* collected on this species carried pollinia. The corpuscula were almost exclusively attached to two body parts: (1) the pulvilli (91.6%) and (2) the mouth parts (8.4%). Of the 7776 pollinial sacs extracted, 4736 (60.9%) were inserted (Table 1).

Eight hundred and sixty-five specimens of *Bombus pennsylvanicus* also were caught on the flowers of this species but only two were found to be carrying pollinia, i.e., one intact pollinia each. A variety of sphecid wasps and butterflies, including the monarch (*Danaus plexippus*), hair streaks (*Strymon sp.*), and skippers (*Epargyreus sp.*), were also collected, but these carried no pollinia. The one specimen of *Sphex ichneumoneus* caught had extracted four pollinial sacs, three of which were inserted.

A. tuberosa (butterfly weed). Observations on 865 flowering stems of this milkweed were carried out through two blooming seasons. As with many of the other species of *Asclepias*, the exotic *Apis mellifera* was the major pollinator for this milkweed. Sixty-nine specimens of this species, carrying 1138 pollinial sacs, were collected from its flowers over two blooming seasons (Table 1). There were 814 pollinial sacs (71.5%) inserted. More than two-thirds of the corpuscula were attached to the tarsal hairs (36.6%) and tibial hairs (29.9%).

Fourteen specimens of *B. pennsylvanicus* were collected on the flowers of *A. tuberosa*. Five of these carried 24 pollinial sacs, of which 12 (50.0%) were inserted. Two specimens of the great golden thread-waisted wasp (*Sphex ichneumoneus*) were collected, each of which carried over 90 pollinial sacs. Of the 218 pollinial sacs extracted, 83.5% (182) were inserted.

Twenty specimens of the leaf cutting bee (*Megachile brevis*) were collected. Only two of these twenty carried pollinial sacs. One specimen carried 4 and the other 6. Only 3 of these were inserted. The little plasterer bee (*Colletes armatus*) was frequently seen visiting the flowers of this milkweed, but only one of the 7 specimens collected carried pollinial sacs. Of the eight pollinial sacs extracted, 6 were inserted.

Many tiny flies (*Diptera*) and wingless ants (*Formicidae*) were observed visiting the flowers, yet none carried pollinia. Butterflies visited the flowers frequently. The hairstreak (*Strymon acadica*) and the monarch (*Danaus plexippus*) were among those observed, but they were almost always free of pollinia. If a pollinium was present, it was usually complete with two pollinial sacs. Many lesser milkweed bugs (*Lygaeus kalmii*) were examined, but only one was found carrying one complete pollinium.

A. verticillata (whorled milkweed). Based on the observations of 15,000 flowering stems over a period of two blooming seasons there appears to be no major pollinator of this milkweed (Table 1). This is in accordance with the work of Willson, Bertin and Price (1979). Thirteen species were collected on it. The most numerous pollinators were the honey bee (*Apis mellifera*), the five-banded tiphiid wasp (*Myzinum quinquecintum*) and the thread-waisted wasps (*Sphex ichneumoneus* and *S. pennsylvanicus*).

Many species of small bees and wasps were common visitors. Lepidoptera were fewer in number and generally smaller in

Table 6. Attachment of Pollinia to the body parts of the swallowtail (*Papilio polyxenes*), the bee (*Anthophora abrupta*), and the wasp (*Myzinum quinquecinctum*) pollinating *Asclepias*.

Body Part	*Papilio polyxenes* (7) *A.incarnata*		*Limenitis archippus* (6) *A.incarnata*		*Anthophora abrupta* (6) *A.meadii*		*Myzinum quinquecintum* (15) *A.verticillata*	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	0	0	0	0	4	0	6	3
Claws								
front	130	105	0	0	0	0	2	1
middle	46	37	0	0	0	0	4	1
hind	26	20	0	0	0	0	2	0
Pulvilli								
front	0	0	0	0	0	0	114	74
middle	0	0	0	0	8	3	54	38
hind	0	0	0	0	12	8	16	14
Tarsi								
front	20	17	0	0	0	0	98	32
middle	66	46	56	42	0	0	206	82
hind	78	57	36	18	0	0	132	92
Tibiae								
front	0	0	0	0	0	0	8	1
middle	4	2	0	0	0	0	0	0
hind	14	4	6	3	0	0	12	3
Thorax	0	0	0	0	2	0	0	0
Totals	384	288	98	63	26	11	654	341
% Transferred	(75.0)		(64.3)		(42.3)		(52.1)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

size on this milkweed than those on the other small flowered marsh milkweed (*A. incarnata*). The orders of Diptera, Coleoptera, and Hemiptera were also represented in collections taken from the flowers, but none of the specimens carried significant numbers of pollinia or had sufficient numbers of pollinial sacs missing as an indication of effective pollination. The largest numbers of pollinia for these species were attached to the tarsal hairs of the insects (Table 5). The average numbers of pollinia carried were much fewer, and the percentages of insertion were also lower for all insects visiting this species as compared to the insects visiting *A. incarnata*.

Many insects collected from *A. verticillata* carried pollinia from *A. incarnata* and/or *A. syriaca* (Table 7). More than half of the specimens of *Sphex ichneumoneus* carried the pollinia of two or three species of *Asclepias*. Two of the 15 specimens of *Myzinum quinquecintum* collected, were found to have pollinia of *A. incarnata* attached, even though none was observed on or collected from flowering stems of that milkweed.

A. viridiflora (small green milkweed). Only 5 specimens of the bumble bee (*B. griseocollis*) were collected on the 83 flowering stems of this milkweed observed during two blooming seasons (Table 1). Of a total of 176 pollinia sacs extracted, 70 were inserted (39.8%). Most of the pollinia (88.7%) were attached to the tarsal hairs of all three pairs of legs. The greatest number was carried on the middle pair with a lesser number on the tarsal hairs of the third pair of legs. Approximately 10.2% were carried by tibial hairs of the front and middle legs. Only one pollinia was attached to the mouth parts.

DISCUSSION

In this study, over 40,000 flowering stems of twelve species of *Asclepias* were observed for possible insect pollinators. The number of flowering stems were not divided equally among these twelve species. Ninety-four percent of the stems observed belonged to three species: common milkweed (*Asclepias syriaca*), whorled milkweed (*A. verticillata*) and marsh milkweed (*A. incarnata*). These species are the most common of the milkweeds forming large colonies with hundreds or even thousands of flowering stems. Also they are the weediest of the milkweeds, growing in early seral stages of succession. Insect visitors are attracted to them, and large numbers of specimens can be collected from them in relatively short periods of time. They provide abundant data for statistical analysis and are usually the species studied by ecologists.

On the other hand with few exceptions, most of the other species of milkweeds are hardly studied at all. They are rare or of uncommon occurrence and grow as widely scattered single plants or in small colonies. They are usually associated with higher seral stages of ecological succession (prairies, savannas, and open woods) or require unusual soils, such as, sand or calcareous gravels. Moreover, very few insect visitors seem to be attracted to their flowers. Only 4 specimens were taken from *A. hirtella*, 9 specimens from *A. meadii*, 2 from *A. lanuginosa*, and 5 from *A. viridiflora* (Table 1). Pod production in these four species of *Asclepias* is usually very poor (Betz and Lamp 1990).

There is some question as to whether the principal pollinators collected on *Asclepias spp.*, and reported in this paper, are the same ones that were the principal pollinators of *Asclepias* in pre-settlement times. This is especially true for the exotic honey bee (*Apis mellifera*). This is almost the exclusive pollinator of *A. syriaca* today, and it accounts for 99.9% of the pollinial sacs that were inserted in that species. This exotic species also appears to be the major pollinator of *A. purpurascens* (82.5%), *A. tuberosa* (80.8%), and *A. sullivantii* (79.06%), and it is relatively important in the pollination of *A. exaltata* (52.5%), *A. incarnata* (24.5%), and *A. verticillata* (11.0%).

If *Apis mellifera* was not in North America in pre-settlement times, what were the principal pollinators of these *Asclepias* species? One possibility is that some of the present-day pollinators, such as bumblebees (*Bombus*), thread-waisted wasps (*Sphex, Tachytes*), and paper wasps (*Vespidae*), may have existed in greater numbers in pre-settlement times than at present. Thus they could have been major pollinators for these species. There is circumstantial evidence that there has been a major decline in native insect populations since settlement (Betz and Lamp 1990). This decline may have been due to: (1) loss of habitat; and/or (2) heavy competition for nectar from the ubiquitous *Apis mellifera* (Paton 1993).

Another possibility is that there may have been other pollinators of *Asclepias* in presettlement times that were then common or even abundant. These pollinators may have suffered precipitous declines in population and thus are rare today. In some cases the presettlement pollinator or pollinators may have been extirpated entirely from the region. The differences in floral displays among *Asclepias* species, such as colors and sizes of the flowers and the wide variation in umbel types, would tend to support such a hypothesis. For example, in some species, such as *A. lanuginosa* and *A. hirtella*, the flowers are small; whereas, in *A. meadii* and *A. sullivantii*, they are fairly large. Many species have purple or pink flowers, as in *A. syriaca* and *A. purpurascens*; whereas, other species have a variety of colors: green in *A. viridiflora*; orange or yellow in *A. tuberosa*; white in *A. verticillata* and *A. exaltata*; and greenish-yellow in *A. meadii*. In some species the flowers have long pedicels arranged in loose umbels, as found in *A. amplexicaulis* and *A. hirtella*; whereas, in others, as shown by *A. viridiflora* and *A. tuberosa*, the flowers have shorter pedicels and the umbels are tight and upright.

The inflorescence of Mead's milkweed (*A. meadii*) may be an example offering support to the hypothesis of pre-settlement pollinators. This species produces a greenish-yellow, flat, and nodding umbel in which the dozen flowers (mean 12, S.D. 3.3) are tightly packed together and lie in the same plane. When pollinators are on it, sucking nectar and presumably pollinating its flowers, they are partially hanging onto the flowers upside down. Was the evolution of this type of floral inflorescence adapted for a "generalist" pollination syndrome or for a specific pollinator? The present study indicates that the uncommon and even perhaps rare mining bee, *Anthophora abrupta* in the family Anthophoridae, may be a principal pollinator of *A. meadii* instead of the more common bumble bees (*Bombus spp.*) (Table 1). This species is robust and hairy and superficially resembles a small bumble bee worker.

Anthophora abrupta and other related anthophorid bees, may have occupied the ecological niches in presettlement times now occupied by *Apis mellifera*. In comparison to the 12 mm. long *Apis mellifera* worker, the body size for *Anthophora abrupta* is slightly larger. The female *Anthophora abrupta* female is 18 mm long, and the male is 13-16 mm (Mitchell 1962). This larger size would enable it to more easily break pollinial translator arms and thus not become entrapped on *Asclepias* flowers as is often the case with the workers of *Apis mellifera* (Robertson 1927). Moreover, while *Anthophora abrupta* is not social like the honey bee, large numbers nest

Table 7. Insects carrying more than one species of *Asclepias* pollinia.

	Apis mellifera (35)	*Bombus griseocollis* (39)	*Myzinum quinquecinctum* (15)	*Sphex ichneumoneus* (37)	*Sphex pennsylvanicus* (26)
A.v+s+i	3	0	0	8	4
A.v+s	3	4	0	2	0
A.v+i	1	2	2	4	4
A.s+i	1	10	0	7	2
Total with different pollinia	8	16	2	21	10
Percent of total collected	23	41	13	57	39

v = *A. verticillata*; s = *A. syriaca*; and i = *A. incarnata*; Sample size (in parentheses).

together in communal burrows in the ground or in clay banks. Thus this species could be an important pollinator in late spring and early summer during this bee's reproductive season (Rau 1929 and Pearson 1933).

Another similarity between *Anthophora abrupta* and *Apis mellifera* is that during the pollination of milkweeds there is a preponderance of the attachment of the corpuscula and chains of pollinia to the pulvilli (Tables 4 and 6). This is in contrast to the bumblebees (*Bombus*) and *Sphex* wasps where the attachment is to the tarsal hairs (Tables 3 and 5). It is possible that the raised anther wings on *Asclepias* flowers may have evolved to guide more effectively the tarsal claws of presettlement pollinators to enable the pulvilli with their chains of pollinia to be directed along the stigmatic slit. The attachment of corpuscula to other parts of the pollinator, such as tarsal and tibial hairs, and their insertion into the stigmatic chambers may be less efficient and more accidental.

Many genera in the Anthophoridae have been reported as visitors, sometimes frequently, to other species of *Asclepias*. Some were observed carrying pollinia. These were: (1) *Anthophora, Tetralonia* on *A. purpurascens*; (2) *Epeolus, Florilegus, Melissodes* on *A. sullivantii*; (3) *Anthophora, Epeolus, Florilegus, Melissodes, Peponapis, Tetralonia, Triepeolus* and *Xenoglossa* on *A. syriaca*; (4) *Melissodes* on *A. tuberosa*; (5) *Ceratina, Melissodes, Triepeolus* on *A. verticillata*; (6) *Anthedonia* on *A. viridiflous* and (7) *Melissodes* and *Svastra* on *A. incarnata* (Robertson 1927). The anthophorid *Melissodes desponsa* was found to be a major pollinator of *Asclepias quadrifolia* in western Missouri (Chaplin and Walker 1982).

There are a number of factors which hinder studies on possible presettlement pollinators of *Aslcepias* species. On the one hand, with the possible exception of the few common species, such as *A. syriaca* and *A. incarnata*, most populations of less common, even rare, milkweeds are declining (Betz 1989, Betz and Lamp 1990). It is questionable if sufficient numbers of plants could be found for these in relatively undisturbed communities (prairies and savannas) in order to collect statistically reliable data. On the other hand, the populations of potential pollinators are low and also possibly declining (Betz and Lamp 1990). Many of the species of bees listed for the Chicago Region (Pearson 1931), and found in the collections at the Field Museum of Natural History, Chicago, Illinois, have not been collected for decades.

Another problem to contend with is the presence of the ubiquitous honey bee (*Apis mellifera*) which would appear to compete with native bees for nectar (Paton 1992). It is interesting to note that this species is presently being parasitized by two introduced mites: (1) the tracheal mite (*Acarapis woodi*); and (2) the ectoparasitic Varrosa mite (*Varroa jacobsoni*). These are causing wide-spread destruction of *Apis mellifera* colonies and may reduce their numbers sufficiently to allow the return of larger populations of native bees.

In recent times, successful efforts have been made throughout the Middle West to restore and enrich tallgrass prairie remnants (Betz 1986). Rare and uncommon prairie plant species are being grown and reintroduced into these preserves with resulting increases in populations. Unfortunately, almost no efforts have been undertaken to reintroduce the apparently regionally exterminated populations of our native insects into these restored preserves. Hopefully, more atten-

tion will be given in the future to the study of the ecological requirements of our native bees so that they can be introduced into prairie and other types of preserves. This could produce ecological communities that would better approximate presettlement communities than those of the present day. This may, in turn lead to the possibility of a better understanding of presettlement pollination ecology.

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LITERATURE CITED

Betz, Robert F. (1986). One decade of research in prairie restoration at the Fermi National Accelerator Laboratory (Fermilab), Batavia, Illinois. *In* Proceedings of the Ninth North American Prairie Conference. *Edited by* Clambey, Gary K. and Richard H. Pemble. Moorhead, Minnesota.

Betz, Robert F. (1989). Ecology of Mead's milkweed (*Asclepias meadii* Torrey). *In* Proceedings of the Eleventh North American Prairie Conference. *Edited by* Bragg, Thomas B. and James Stubbendieck. Lincoln, Nebraska. pp. 187-191.

Betz, Robert F. and Herbert F. Lamp (1990). Flower, pod, and seed production in eighteen species of milkweeds (*Asclepias*). pages 25-30. *In* Proceedings of the Twelfth North American Prairie Conference. *Edited by* Smith, Daryl D. and Carol A. Jacobs Cedar Falls, Iowa. pp. 25-30.

Brookman, Susan S.(1981). The flora morphology of *Asclepias speciosa* (*Asclepiadaceae*) in relation to pollination and a clarification in terminology for the genus. American Journal of Botany 68(5):675-679.

Brown, R. 1831. On the organs and mode of fecundation in *Orchideae* and *Asclepiadeae*. Transactions of the Linnean Society 16:683-746.

Chaplin, Stephen J. and John L. Walker. 1982. Energetic constraints and adaptive significance of the floral display of a forest milkweed. Ecology 63(6):1857-1870.

Corry, T.H. 1883. On the structure and development of the mode fertilization of *Asclepias Cornuti Decaisne* (*A.syriaca*). Transactions of the Linnean Society of Botany 2:173-208.

Delpino, F. 1867. Sugli apparechi delia fecondazione nelle piante antocarpee (fanerogame). Cellini, Firenze.

Frost, S.W. 1965. Insects and pollinia. Ecology 46(4):556-558.

Frye, T.C. 1902. A morphological study of certain *Asclepiadaceae* , Botanical Gazette 34:389-413.

Heitler, Francis B. 1968. Unpublished data.

Hildebrand, F. 1866. Ueber die Befruchtung von *Asclepias Cornuti*. Botanische Zeitung 24:376-378.

Mueller, H. 1873. Die Befruchtung der Blumen durch Insekten. Engelmann, Leipzig.

Mueller, H. 1882. Weitere Beobachtungen ueber Befructung der Blumen durch Insekten. III. Verhandl. des naturhist. Ver. der preuss. Rheinl. u. Westfalens 39:1-l04.

Macior, Lazarus W. 1965. Insect adaptations and behavior in *Asclepias* pollination. Torrey Botany Club Bulletin 92(2):114-126.

Paton, David C. 1993. Honeybees in the Australian environment. BioScience 43 (2):95-103.

Pearson, Jay F.W. 1933. Studies on the ecological relations of bees in the Chicago region. Ecological Monographs 3 (3):373-441.

Rau, Phil. 1929. The biology and behaviour of mining bees, *Anthophora abrupta and Entechnia taurea*. Psyche 36(3):155-181.

Robertson, Charles. 1886. Notes on the mode of pollination of *Asclepias*. Botanical Gazette 11(10):262-269.

Robertson, Charles. 1887a. Insect relations of certain Asclepiads. I. Botanical Gazette 12(9):207-216.

Robertson, Charles. 1887b. Insect relations of certain Asclepiads. II. Botanical Gazette 12(10):244-250.

Robertson, Charles. 1891. Insect pollinators of *Asclepias*. Transactions of the Academy of Science at St. Louis. 5:569.

Robertson, Charles. 1927. Flowers and insects. Science Printing Company. Lancaster, Pennsylvania.

Sprengel, C.K. 1793. Das endeckte Geheimniss der Nature in Bau and in der Befruchtung der Blumen. Vieweg, Berlin.

Struven, Roy D. 1972. A study of the insect pollinators of four species of *Asclepias*. Master's Thesis, Northeastern Illinois University, Chicago, Illinois.

Wall, James E. 1968. A study of the insect pollinators of four species of *Asclepias*. Master's Thesis, Northeastern Illinois University, Chicago, Illinois.

Willson, M.F. and R.I.Bertin. 1979. Flower visitors, nectar production, and inflorescence size of *Asclepias syriaca L.* Canadian Journal of Botany 56:1380-1388.

Willson, M.F., R.I.Bertin, and P.W. Price. 1979. Nectar production and flower visitors of *Asclepias verticillata*. American Midland Naturalist 102(1):23-35.