

Principal Sunflower Bees of
North America with Emphasis on
the Southwestern United States
(Hymenoptera: Apoidea)

PAUL D. HURD, JR.,
WALLACE E. LaBERGE,
and
E. GORTON LINSLEY

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ABSTRACT

Hurd, Paul D., Jr., Wallace E. LaBerge, and E. Gorton Linsley. Principal Sunflower Bees of North America with Emphasis on the Southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology*, number 310, 158 pages, 1 frontispiece, 11 figures, 5 plates, 17 tables, 1980.—This investigation focuses primarily on those ecological and evolutionary aspects involved in the natural history of the bees that utilize the pollen, nectar, or both, of sunflowers (*Helianthus*) in North America either for their survival as species or for their maintenance in viable populations. This bee-flower association is examined principally by analyses of the intrafloral, geographic, diurnal, and seasonal interrelationships that exist between this fauna of bees and the various species of *Helianthus* present in North America. On the basis of this study it is established that more than 400 species of native bees visit the flowers of *Helianthus* in America north of Mexico. Of these it is those species that have evolved a specialized intrafloral relationship with these flowers that serve as the principal pollinators of these plants.

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FRONTISPIECE.—*Megachile parallela* Smith (female) on flower of *Helianthus*.

Principal Sunflower Bees of North America with Emphasis on the Southwestern United States (Hymenoptera: Apoidea)

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Introduction

The population aspects of bee-flower relationships in the southwestern United States, especially interspecific competition among pollen- and nectar-seekers, have been studied for certain species in such diverse plant groups as the matinal flowering *Camissonia*, *Cucurbita*, *Solanum*, *Cassia*, and *Kallstroemia*, the late afternoon flowering *Mentzelia*, and the evening flowering *Oenothera*, where competition is often intense during the short diurnal blooming period (Linsley, 1978). Only recently have quantitative data become available on pollen and nectar utilization among flower visitors to plants that present nectar and pollen throughout the day (e.g. *Larrea*, Hurd and Linsley, 1975; *Clarkia*, MacSwain et al., 1973).

Clarification of the roles and competitive relationships of oligoleges, regular polyleges, and casual polyleges has provided new insights into uni-

lateral and coevolution in insect-flower relationships. Perhaps the most characteristic and neglected of "all-day" plants in these regards are the sunflowers (*Helianthus* spp.), which provide a continuously favorable environment for pollen- and nectar-seeking bees, both of which are capable of providing cross-pollination.

Heiser et al. (1969), in the most recent monograph of North American sunflowers, state that with the exception of *H. agrestis* and a certain cultivated strain of *H. annuus*, all species of *Helianthus* are self-incompatible and cross-pollination is obligate, and that no detailed study of pollinators has been made other than for cultivated forms of *H. annuus* (Free, 1964). These authors remark, however, that from observations in the field and in the experimental garden it is obvious that the principal pollinators are bees, including the introduced European honeybee. They note that butterflies visit sunflowers extremely rarely, and that their occasional visits have usually been to the pale primrose form (or strain) of *H. debilis* ssp. *cucumerifolius*.

While it is technically true that no detailed general study of *Helianthus* pollinators has been

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made (and this actually applies to the cultivated strains of *H. annuus*), several preliminary lists of sunflower visitors in various parts of the country have been published (see "Intrafloral Relationships of Bees Associated with *Helianthus*" herein). These, along with scattered data in entomological monographs and local lists, as well as preliminary samples taken by us in 1973 and 1974, indicated that quantitative studies on diurnal and seasonal cycles and interspecific competition among bee visitors would hold promise of yielding interesting ecological and evolutionary data.

Reports concerning bees visiting particular species of Compositae in the southwestern United States are very few. Butler, Werner, and Levin (1966) made twelve locality-month collections in commercial fields of safflower (*Carthamus tinctorius*) in south central Arizona (primarily Tucson and vicinity) in late May and June. Although they report finding 40 species of native bees, excluding parasitic bees (actually, their list includes four species of cleptoparasitic *Sphcodes*), they record the sex of the bees only in the case of *Agapostemon texanus* and do not indicate which species were taking pollen. (In a companion paper, Levin and Butler, 1966, describe their sampling methods, times of day and length of the sampling periods).

Although the taxonomic representation among polyleges partial to safflower is not unlike that which we have found in the same general area on *Helianthus annuus* and *Verbesina encelioides*, e.g. mainly halictids (*Halictus*, *Lasioglossum*, *Evyllaes*, *Dialictus*, and *Agapostemon*), megachilids (*Ashmeadiella* and *Megachile*), Anthophoridae (*Melissodes*, *Anthophora* and *Xylocopa*), and Apidae (*Bombus*), the number of consistent visitors to the introduced safflower is considerably smaller than is usual for such native composites as sunflowers (*Helianthus* spp.), which reach their peak of nectar and pollen production in the period of July to September.

This project, following the methodology utilized by Hurd and Linsley (1975) in their recent treatment of *Larrea* bees, studied the diurnal, seasonal, and geographical occurrence of the principal bees visiting *Helianthus*. Primary emphasis was placed on the southwestern United States from the Upper Rio Grande Valley of New Mex-

ico to the upper Mojave, the Colorado Desert, and the San Joaquin Valley of California. Specific objectives of this study were to determine the extent to which pollinators are specific to, or show a marked preference for, *Helianthus*, and to quantify data on interspecific competition among pollinators. Cockerell (1914b) has correctly remarked that male bees visiting sunflowers get covered with pollen, and must be almost as useful as females in the pollination of sunflowers. Thus we have included records of floral visits of male bees and nectar-seeking females as well as females that gather pollen.

Unfortunately, the manuscript was completed before the important and valuable book by Heiser (1976) entitled *The Sunflower* was received. Although we have tried to incorporate the findings reported therein, we have been unable to provide references to this work as uniformly as that work deserves. The same is true of *Sunflower Science and Technology* edited by Carter (1978).

METHODS OF STUDY.—The chief sources of data utilized in this study are published records of North American bees collected at *Helianthus* flowers, records obtained from specimens in museum collections, and especially our intensive field surveys and samples of bees at the flowers of *Helianthus* during the years of 1973–1977 in Arizona, California, and New Mexico. Of the literature records, we have cited primarily those that can be interpreted in terms of objectives of the project. Unfortunately some of these do not indicate whether or not visitors at the flowers of *Helianthus* were actually taking pollen.

Our field surveys and sampling of bees from *Helianthus* flowers have been directed primarily at desert areas in the southwestern United States and the cismontane areas of California including the San Joaquin Valley and coastal southern California. Analyses of data assembled from these various sources have been accomplished primarily by mapping and by plotting the frequency of collection of bees from the flowers of *Helianthus* in relation to other plant species and the proportion of females carrying *Helianthus* pollen against foreign pollens or no pollen at all. Relative frequencies of *Helianthus* flower records have permitted

preliminary judgments as to whether the bee species are pollen specialists (oligoleges) or pollen generalists (polyleges) and estimates of their probable value as pollinators.

For data extracted from published records and museum specimens we have used the taxa of *Helianthus* as reported by the authors or collectors. Although *H. lenticularis* is currently regarded as a synonym of *H. annuus* (Heiser, 1976), we have listed data for *H. lenticularis* separately in Table N and elsewhere because of the large number of records published under this name.

SAMPLING PROCEDURES.—Bees visiting sunflowers were sampled in the manner utilized by Hurd and Linsley (1975) in their study of *Larrea* bees. The bees were collected continuously in half-hour periods, and no bee was taken until it actually alighted on or was seen to visit a flower. This tended to result in an under-sampling of males of oligoleges that patrolled the flower, stopping for nectar only when it was needed for a fresh supply of energy. To minimize error in marking collection vials in the field and in labeling subsequently mounted specimens, the periods were actually recorded as 30 minutes each. Each period, however, started on the hour or half-hour (0600, 0630, etc.) and ended 29 minutes later when vials and labels were changed (0629, 0659). When the collection records were transcribed for analysis they were converted to 29-minute periods. Time periods are reported as Standard Time. Air temperatures were taken in the shade and recorded at the beginning of each sampling period.

The following initials are used in the species accounts for the principal collectors: Paul D. Hurd, Jr. (PDH), E. Gorton Linsley (EGL), Juanita M. (Mrs. E. G.) Linsley (JML), A. E. Michelbacher (AEM), and Martha M. (Mrs. A. E.) Michelbacher (MMM).

In the tables of collections from sampling sites (Tables A-M in the Appendix) the following abbreviations are used: P = carrying *Helianthus* pollen in the scopa, N = ♀ or ♂ taking nectar only, although either may be dusted with *Helianthus* pollen beneath and the female may be carrying pollen from some other plant in the scopa. Each column is headed with the beginning and

ending time of the sample period and the air temperature expressed as °C. Observation periods in which bees in one or another category were not captured are indicated by a dash (-), periods in which no sampling was attempted, for personal reasons or for adverse weather conditions, are indicated by an asterisk (*). Bees sleeping on flower heads were sampled in comparative but small numbers, so as not to affect materially subsequent activity counts. They are not included in the flower visiting totals. All female honeybees reported were workers, as were bumblebees unless otherwise specified.

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Ms. Emma Kiesel of Oakland, California, for locating the sunflower site at Escalon, California, where we were able to obtain a valuable time count (Table M).

Throughout the course of the project we have relied upon P. H. Timberlake of the University of California, Riverside, for identification or verification of identifications of certain groups of bees, especially *Exomalopsis*, *Perdita*, and *Pseudopanurgus*. We also wish to acknowledge the identifications supplied by the following: Howell V. Daly, University of California, Berkeley (*Ceratina*); George E. Eickwort, Cornell University, Ithaca (Halictines, especially *Dialictus*); Frank D. Parker, USDA SEA Bee Biology and Systematics Laboratory, Utah State University, Logan (*Ashmeadiella*); and Robbin W. Thorp, University of California, Davis (*Bombus*).

In the preparation of the maps (Figures 2-6, 8-11) we received much assistance from a number of individuals who supplied information for certain of these figures. We would therefore like to express our thanks to P. H. Timberlake for supplying locality data for *Pseudopanurgus aethiops* (Figure 3) and *Nomia heteropoda* (Figure 5) and to the following who furnished us with additional locality data for Figure 5: W. F. Barr, University of Idaho, Moscow; George W. Byers, University of Kansas, Lawrence; Wilbur R. Enns, University of Missouri, Columbia; Marjorie Favreau, American Museum of Natural History, New York; Gary F. Hevel, National Museum of Natural History (NMNH), Smithsonian Institution, Washington; Carl A. Olson and Floyd G. Werner, University of Arizona, Tucson; J. A. Powell and J. A. Chemsak, University of California, Berkeley; Roy R. Snelling, Los Angeles County Museum of Natural History, Los Angeles; Davis L. Stephan, North Carolina State University, Raleigh; and Robbin W. Thorp and Stephen L. Buchmann, University of California, Davis.

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We are indebted to Edward S. Ross, California Academy of Sciences, San Francisco, for the photographs reproduced in the frontispiece and in Plates 1-3. Similarly we acknowledge our indebtedness to Dennis L. Briggs, University of California, Davis, for the photographs reproduced in Plates 4-5.

Throughout the course of the project we have been ably assisted in a variety of capacities by Kathleen Sorensen of the University of California, Berkeley. She has extracted much of the data from various collections, prepared the maps that accompany this study and has performed most of the preparation and curation of the specimens obtained during our field investigations.

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bodied in the data base for "Superfamily Apoidea," *Catalog of Hymenoptera in America North of Mexico* (Hurd, 1979).

Principal Sampling and Survey Sites

For our field investigations of the intrafloral relationships of the bees associated with *Helianthus*, we selected 8 primary study sites for an intensive sampling and survey program in the southwestern United States (Tables A-M, in Appendix). These sites were chosen to represent as nearly as possible an east-west transect extending from western New Mexico across Arizona into cismontane southern California with this western terminus expanded northward into the Mojave Desert and the Great Valley of California (San Joaquin Valley).

These primary study sites and some others chosen at random in Arizona and California are

grouped for discussion in this section into regions largely on the basis of ecogeographic similarities. The regions are arranged sequentially from east to west within each of the four major subdivisions of the total area studied: Chihuahuan Desert, Sonoran Desert, Mojave Desert, and cismontane California. In Table 1 we have listed those regions where time counts were made (Tables A-M) and have tabulated by study sites the numbers of specimens taken at these sites.

Summarized in Table 2 are the numbers of individuals for each of the 17 commonest pollen-collecting species of bees that were taken during our surveys at the primary sampling and survey sites in New Mexico, Arizona, and California (Tables A-M). From the foregoing it is readily apparent that the 17 commonest species of *Helianthus* bees (9036 specimens) represent more than 90 percent of the total specimens of bees (9964) obtained in the time counts during our

TABLE 1.—Number of specimens collected in primary surveys, arranged by regions and study sites

<i>Regions and study sites</i>	<i>Females</i>	<i>Males</i>	<i>Totals</i>
Vargus Valley, New Mexico Silver City (Table A)	150	24	174
Animas Valley, New Mexico Animas (Table B)	587	508	1095
San Simon Valley, New Mexico Rodeo (Table C)	1371	588	1959
Sulphur Springs Valley, Arizona Double Adobe (Table D)	445	165	610
San Pedro River Valley, Arizona Benson (Table E)	102	109	211
Coachella Valley, California Indio (Table F)	169	333	502
Owens Valley, California Bishop (Table G)	124	140	264
San Joaquin Valley, California			
{Corcoran (Table H)	122	555	677
{Madera (Tables I-K)	1973	757	2730
{Merced (Table L)	251	87	338
{Escalon (Table M)	645	759	1404
} 2291		2158	5149
<i>Totals</i>	5939	4025	9964

TABLE 2.—Number of specimens of 17 commonest pollen-collecting species of bees taken at survey sites

Species	Females		Males	Total specimens	Number of sites
	(pollen)	(nectar)			
<i>Diadasia enavata</i>	1333	200	1270	2803	7
<i>Melissodes agilis</i>	690	176	1061	1927	13
<i>Svastra obliqua</i>	775	130	295	1200	10
<i>Svastra machaerantherae</i>	291	80	299	670	4
<i>Megachile parallela</i>	332	192	42	566	10
<i>Halictus ligatus</i>	220	38	195	453	12
<i>Melissodes tristis</i>	6	22	247	275	5
<i>Nomia heteropoda</i>	122	14	114	250	4
<i>Bombus pennsylvanicus sonorus</i>	32	106	45	183	13
<i>Agapostemon angelicus</i>	101	35	24	160	4
<i>Megachile inimica</i>	59	69	6	134	4
<i>Melissodes lupina</i>	27	57	8	92	5
<i>Pseudopanurgus aethiops</i>	22	7	61	90	5
<i>Andrena accepta</i>	34	3	34	71	6
<i>Melissodes submnuacha</i>	30	4	28	62	3
<i>Melissodes montana</i>	23	1	34	58	5
<i>Megachile pollicaris</i>	4	9	29	42	4
Totals	4101	1143	3792	9036	13

sampling program at the eight primary study sites (Tables A-M).

The following accounts briefly characterize by regions, proceeding generally from east to west, the principal sampling and survey sites of our field program.

CHIHUAHUAN DESERT

Vargus Valley: Silver City, Grant County, New Mexico (Table A). Located approximately 90 km northeast of Deming, this one time gold, silver, and zinc mining town is now a flourishing city and trading center for cattle ranching and copper mining. Our samples were taken at an elevation of 1798 m, 8 km northwest of the city in a roadside ditch where a dense stand of *Helianthus petiolaris* was growing. Broken skies and afternoon rains inhibited sampling on the two days available, 11–12 September 1974. Only 174 bees were collected in nine half-hour counts between 0730 and 1600 hrs conducted when conditions were satisfactory for bee activity. The sample,

nevertheless, included 26 species of bees, of which 103 were females taking pollen. The most prominent among these were *Megachile inimica* (which represented 40 percent of all the pollen collectors), *M. parallela* (15 percent), *Melissodes montana* (12 percent), *Megachile agustini* (7 percent), *Melissodes sonorensis* (6 percent), *Syntrichalonia exquisita* (4 percent), and *Svastra obliqua* (4 percent). Only 3 female *Melissodes agilis* were captured and none was taking pollen. This fact and the presence of relatively few *Svastra obliqua* suggest that either the season was just starting or that these species prefer *Helianthus annuus*, which was present in several areas in the vicinity of the city but was not yet in bloom.

Animas Valley: Animas, Hidalgo County, New Mexico (Table B). A small town in an agricultural community in the Animas Valley just east of the Pelancillo Mountains, at an elevation of 1341 m. Twenty-six half-hour samples were taken from *Helianthus annuus* near the edge of the town along the western shoulder of the highway heading northward to Cotton City. The counts were

made over a two-day period without duplication of samples. More than 1,000 specimens were captured representing 43 species, of which females of at least 17 were taking pollen. The most numerous of these female pollen collectors were *Megachile parallela*, *Melissodes agilis*, *Svastra machaerantherae*, and *Svastra obliqua*. As at other desert localities, the females of *Melissodes agilis* were bimodal in their pollen collecting activity. Of 87 individuals, 58 took pollen between 0600 and 0900 hrs (37 of these between 0700 and 0800) and 29 between 1630 and 1830. Males of *M. agilis* were distributed rather evenly throughout the day patrolling the flowers but the 120 specimens were captured only when they paused for nectar. The most abundant males (210) were those of *Melissodes tristis*, the females of which are polylectic but were taking only nectar from the sunflowers.

San Simon Valley: Rodeo, Hidalgo County, New Mexico (Table C). A former railroad town on U.S. Highway 80, west of the Pelancillo Mountains in the San Simon Valley near the Arizona State border. The collection site was an established *Helianthus annuus* area one mile south of town in a seepage ditch just off the easterly edge of the highway shoulder, which received moisture from an old earthen-walled water tank. The plants were growing in a strip approximately 25 m long by 4–6 m wide, interspersed with dead stalks from previous years. When sampled on 2 September 1973, the plants had been in bloom for 6–8 weeks. The large number of parasitic bees present, especially *Triepeolus*, indicated that the bee populations were well established in the vicinity. Also, annual Compositae which had been in bloom earlier were largely gone to seed, making the sunflowers especially attractive to polylectic species.

The site was first visited at dawn but no bees were present until 30 minutes after sunrise. The first arrivals were pollen-collecting females of *Melissodes agilis* and *Agapostemon angelicus*. These also reappeared and took pollen late in the day. *Svastra* and *Megachile* were dominant between 0800 and 1800. Male *Svastra* and *Melissodes* patrolled the flowers most of the day, but were captured only when they paused on the flowers for nectar.

Of 1959 bees representing at least 54 species collected from the flowers between 0640 and 1900 hours, 849 (43 percent) were females taking pollen. The most numerous of these were *Svastra machaerantherae* (29 percent of all pollen gathering females), *Melissodes agilis* (18 percent), *Megachile parallela* (15 percent), *Svastra obliqua* (12 percent), *Agapostemon angelicus* (9 percent), and *Melissodes submenuacha* (4 percent).

Duncan Valley: Franklin, Graham County, Arizona. Collections were made from a strip of sunflowers (*H. annuus*) growing along the edge of a dry streambank about 7.5 m from the edge of the highway.

Sulphur Springs Valley: Double Adobe, Cochise County, Arizona (Table D). This locality, northwest of Douglas, is located in agricultural and range land and our collecting site was in a drainage ditch on the easterly edge of the highway just north of this small settlement. Sampling was difficult because of water in the ditch and the fact that most of the flowers faced eastward away from the very narrow highway shoulder. Thus, although consecutive all-day counts were not feasible, collections were taken from time to time and are recorded as a composite sample that gives an indication of the variety of species present. Collections were also made near Cochise, Cochise County, in roadside stands of *H. annuus* and were recorded but not tabulated.

San Pedro River Valley: Benson, Cochise County, Arizona (Table E). A modernized railroad town on Interstate Highway 10 in west central Cochise County about one-fourth of the distance between Tucson, Arizona, and Lordsburg, New Mexico. Samples were taken from a row of *Helianthus annuus* in a vacant lot near the edge of town on 14 September 1974. Although temperatures were adequate for flight, broken sky and clouds at midday and rain in the late afternoon precluded a full-day count; nevertheless, 211 individuals were captured between 0715 and 1430 hrs, of which 75 were pollen gathering females. *Melissodes agilis*, as usual, was the first to appear in the morning, all 43 females taking pollen between 0715 and 0930; 31 of these were active between 0800 and 0900 (rain prevented the normal late afternoon

pollen flight). *Pseudopanurgus aethiops*, *Andrena accepta*, and *Halictus ligatus* were active primarily in the forenoon but this may have been the result of unstable afternoon weather. This was the only sunflower locality sampled in Arizona where a varied representation of bees were present and no *Megachile* appeared.

SONORAN DESERT

Santa Cruz River Valley: 1. Sonoita, 16 km E, Santa Cruz County, Arizona. At this locality, in the northeastern corner of the county, stands of *Helianthus petiolaris* were numerous along State Highway 82, with some mixed groups containing *H. annuus* and scattered small but pure stands of *H. annuus*. On 7 September 1977, sampling revealed that essentially the same species of bees were visiting both species; in mixed stands, individual bees were seen to move from one sunflower to another without hesitation. Pollen collecting was hindered, however, by the large numbers of cantharid beetles, *Chauliognathus basalis* Le Conte and *C. marginatus* (Fabricius), and mirid bugs, *Adelphocoris superbus* (Uhler), on the flower heads, making adequate sampling difficult and an all-day count unfeasible.

2. Patagonia and vicinity, Santa Cruz County, Arizona. From Patagonia northeastward toward Sonoita, *H. annuus* was just coming into full bloom in early and mid-September 1977. Stops were made at several sites up to six miles northeast of town and at each site bumblebees (*Bombus pennsylvanicus sonorus*) were literally swarming about the plants, often with two or three individuals taking nectar from a single flower head. Although a few other sunflower bees were captured, consistent sampling was impossible because of the large number of bumblebees present on the flowers.

3. Nogales, Santa Cruz County, Arizona. Just north of the city on U.S. Highway 18, a large stand of sunflowers was sampled in a vacant lot adjacent to an outdoor motion picture theater. *Bombus* workers were very abundant, mostly taking pollen, and could not be included proportionately in half-hour samples. Other sunflower bees

were well represented but more difficult to capture than usual because of disturbance by the bumblebees and a large number of grasshoppers, *Melanoplus femur-rubrum* (DeGeer) (det. W. W. Middlekauff) which crawled up the stems and onto the flowerheads where they apparently both lapped up nectar and fed on pollen. Half-hour samples of bees, nevertheless, were taken and recorded.

4. Sahuarita, Pima County, Arizona. At this site, samples were taken at noon on 15 June from scattered plants of *H. annuus* growing along a fence row adjacent to a pecan orchard. Only *Diadasia enavata* females were gathering pollen, but both sexes of *D. rinconis*, a cactus oligolege, were present in numbers seeking nectar. When a collection was made on 26 June at noon, no bees were taking pollen. Both sexes of *Diadasia rinconis*, *Megachile texana*, and *Melissodes paroselae*, however, were sipping nectar along with a female *Diadasia enavata* and numerous males of *Melissodes tristis*.

5. San Xavier, Pima County, Arizona. Collections made just after noon on 19 September from sunflowers (*H. annuus*) growing in an agricultural area adjacent to the Santa Cruz River where harvest had been completed. Only three of the bees captured were taking pollen. The principal species present, represented by one or both sexes, were *Melissodes agilis*, *Svastra machaerantherae*, *Halictus confusus*, *H. ligatus*, *Dialictus* sp., *Agapostemon cockerelli*, *Megachile pollicaris*, and *M. occidentalis*.

6. Rillito, 10 km W, Pima County, Arizona. Between 0830 and 0930 27 June females of *Diadasia enavata* and *Svastra obliqua* were taking pollen and/or nectar from *H. annuus* growing on a roadside dampened by irrigation drainage. Both sexes of *Melissodes paroselae* and *M. tristis* were taking nectar.

7. Marana, Pima County, Arizona. Samples were taken from sunflowers (*H. annuus*) growing along a roadside in an agricultural area devoted to field crops. Adequate moisture was provided by irrigation drainage. Between 1030 and 1100 on 27 June no bees were taking pollen. Nectar seekers included both sexes of *Svastra obliqua* and *Megachile parallela*, females of *M. pollicaris*, and males of *M. sidalceae* and *Melissodes paroselae*.

8. Eloy, Pinal County, Arizona. Samples were taken in an agricultural area on the edge of U.S. Interstate Highway 10, from *Helianthus annuus* growing along a fence adjacent to irrigated cultivated fields. Collections were made near mid-day on 14 June (temperatures 41.0°–41.5° C) and the principal bees taking pollen were females of *Diadasia enavata* and *Megachile sidalceae*. Males of these species and *M. gentilis* were also present.

Lower Colorado River Valley: 1. Theba, Maricopa County, Arizona. Collections were made on 28 June from sunflowers (*H. annuus*) growing along the edge of irrigated fields. Females and males were taking nectar during mid- and late morning. Males of *Diadasia enavata*, *Svastra helianthelli*, and *S. obliqua* were predominant, although *Halictus ligatus* and *Megachile sidalceae* were represented.

2. Tacna, Yuma County, Arizona. Collections were made at about 1300 on 28 June (temperature 44° C) from plants of *H. annuus* growing along an irrigation ditch. Only male bees were present, *Svastra helianthelli*, *S. obliqua* and *Megachile sidalceae*.

3. Wellton, Yuma County, Arizona. Samples were taken from scattered plants of *H. annuus* growing along the edge of citrus orchards. At 1100 on 5 September (temperature 37° C), males of *Diadasia enavata* and *Svastra helianthelli* were the predominant bees active, although nectar-gathering females of *Halictus ligatus* and *Tripeolus* were represented.

4. Yuma, Yuma County, Arizona. Collections were made from *H. annuus* growing in harvested cropland adjacent to U.S. Highway 8.

5. Blythe, Riverside County, California. Samples were taken in lower irrigated areas where plants of *H. annuus* were growing along fence rows and ditch banks.

Imperial Valley: Highway 8 from W of El Centro to Holtville, Imperial County, California. Sample sites were confined to irrigated agricultural lands, and collections were made from sunflowers (*H. annuus*) that were growing along fence rows, irrigation ditches, highway shoulders, and drainage areas.

Coachella Valley: Indio, Riverside County, California (Table F). Small samples of bees were

taken on various dates and at various times from *H. annuus* growing along roadside ditches near the edge of the towns of Indio and Coachella. The largest collection (Table F), however, was made from plants growing in a recently cleared Indio citrus orchard from which the trees had been removed but dried fruits not fully decomposed still lay on the ground. Weeds were taking over the field and sunflower was the dominant plant. The most abundant sunflower pollinators at this site were *Nomia heteropoda* (see comments in the species account). This was one of the few sampling sites where significant numbers of worker honeybees were taking sunflower pollen.

MOJAVE DESERT

Owens Valley: 1. Tuttle Creek, 6 km W of Lone Pine, Inyo County, California. Samples were taken from a strip of *H. annuus* growing along the edge of a winding road that followed the course of a stream down the canyon toward Lone Pine.

2. Big Pine, Inyo County, California. The site (elev. 1219 m) at this locality was east of town and consisted of plants growing along a fence marking the edge of a road right-of-way. The dominant species was *Bombus pennsylvanicus sonorinus*. Workers were present in large numbers, some taking pollen, along with nectar-seeking males. They made it difficult to sample other species, which they frequently displaced on the flower heads.

3. Bishop, Inyo County, California (Table G). Sunflowers growing in a vacant lot (elev. 1292 m) at the north end of town provided the sampling site at this locality. *Melissodes agilis* was the principal pollinator present on 27 August 1977 and was the first to appear in the morning, which is its usual period for gathering pollen. Other sunflower bees, however, including *Diadasia enavata*, appeared as the day progressed.

CISMONTANE CALIFORNIA

Coastal Southern California: 1. U.S. Highway 8 at Laguna Junction, San Diego County, California. Samples were collected from the flowers of *H.*

gracilentus, which was growing along the roadside. The most abundant species at the flowers were *Anthophora curta* and *Halictus farinosus*.

2. Newport Beach, Orange County, California. Plants of *H. annuus* were growing in household gardens, and a large collection was made in an uncultivated field adjacent to the beach. Samples were taken at Costa Mesa and the University of California at Irvine, roadside areas, cultivated fields, and uncultivated areas adjacent to cultivated fields. Also collections were made in canyons in hilly regions and areas where growth was encouraged by favorable drainage conditions.

3. Pico Rivera, Los Angeles County, California. Samples were collected from the flowers of *H. annuus* growing in gardens and along roadsides in this metropolitan area.

4. Big Tujunga Canyon and vicinity, Los Angeles County, California. Collections were made from plants of *H. annuus* in isolated areas along the roadsides.

5. Calabasas, Los Angeles County, California. During late September and early October samples were taken from scattered plants of *Helianthus* growing along roadsides and in uncultivated fields in both residential and commercial areas.

6. Gorman, Los Angeles County, California. Samples were taken both from isolated plants and some dense stands of *Helianthus* growing in uncultivated fields and along roadsides.

San Joaquin Valley: 1. Bakersfield and vicinity, Kern County, California. Samples were taken on *H. annuus* along U.S. Highway 99 in a fence row adjacent to an alfalfa field. In the area east of the highway near and along Copus Road, a large collection was made from the flowers of *H. annuus* growing in an onion field that was ready for harvest. Samples were also taken from the flowers located at the edge of a vineyard and in a nearby uncultivated area.

2. Coalinga and vicinity, Fresno County, California. Collections were made along U.S. Interstate Highway 5 on flowers of *H. annuus* growing along the roadsides, about fence rows, ditch banks, and the edges of irrigated fields proceeding

southward into Kern County on the way to Grapevine, the entrance to Tejon Pass.

3. Parlier, Fresno County, California. Collections were made at this locality from the flowers of *H. annuus* growing in a deep sandy wash that was being mined for industrial sand.

4. Corcoran, Kings County, California (Table H). At this locality collections were made late in the season along a roadside ditch in an agricultural and grazing area. *Diadasia enavata* represented more than 50 percent of the bees present. Unexpectedly, however, of 357 individuals taken, 349 were freshly emerged males. Likewise, of 238 *Halictus ligatus*, 184 were males.

5. Madera, Madera County, California (Tables I-K). Three collections were made at this city: on 24 July 1977, 21 September 1977, and 5 October 1975. The July and September collections, made about a month apart, were from a strip of *H. annuus* growing along an irrigation ditch beyond the shoulder of a north-south highway 6 km west of the center of town. On both of these dates *Diadasia enavata* were extremely abundant and completely dominated the flower heads. In October two years earlier, samples were taken from a vacant lot, since cleared for expansion of a residential area, one mile west of the center of the city. At this time the sunflower visitors were more varied, although *Melissodes agilis*, *Svastra obliqua*, and *Diadasia enavata* each made up about 25 percent of the bees present. These three species, however, were not equally distributed throughout the field, which was nearly a city block in size with somewhat separated, but extensive, groups of plants. Four collectors worked primarily in four different stations, thus attempting to assure adequate representation of the species present in the total area.

6. Atwater, Merced County, California. Samples were taken from the flowers of *H. petiolaris* growing in and about recently plowed fields and vacant lots.

7. Merced, Merced County, California (Table L). Samples were taken from *H. annuus* at the edge of a refuse recycling collection site in the northern part of town near the main highway.

On 4 October 1975 *Svastra obliqua* was the dominant bee (constituting more than fifty percent of the sample), followed by *Melissodes agilis* (nearly twenty-five percent), and several other typical sunflower bees.

8. Escalon, San Joaquin County, California (Table M). A large vacant lot in the southern part of the town was the site selected for *H. annuus* sampling at this locality. The plant grew in a fairly solid strip along the western edge of the lot, strung out in a north-south direction and obtaining full exposure to the sun throughout the day. Collections were made on 22 July 1977. The principal species active were the characteristic *Svastra obliqua*, *Melissodes agilis*, and *Diadasia enavata*, but others were also represented.

9. Byron and vicinity, Contra Costa County, California. A number of collections were made along California State Highway 24 from the flowers of uncultivated *Helianthus annuus* growing in roadside situations. On Victoria Island, approximately 0.8 km east of Old River, samples were taken from the flowers of commercially grown sunflowers (*H. annuus* f. *megacarpus*). Due to the density of the planting it was possible to sample only the flowers at or near the edge of the field.

Primary Host Plant

The species of *Helianthus* are native to the Western Hemisphere where the majority of the species, about 50, occur in North America transcontinentally from southern Canada to south-central Mexico and an additional 18 species are present in northwestern South America (Heiser et al., 1969).

STRUCTURE OF THE SUNFLOWER, SELF COMPATIBILITY, AND CROSS POLLINATION.—Hurt (1948: 47) describes some of the remarkable characteristics of the sunflower as follows:

The sunflower (*Helianthus annuus*) belongs to the largest natural order of flowering plants, the Compositae, which are characterized by the crowding together of individual flowers into heads. The heads of the Compositae are surrounded by an involucre or rosette of green bracts, which protect the unopened buds and perform the usual function of a calyx. The flowers open in centripetal succession, from the outer ring inwards (this showing why the central portion of the

head is also the last to shed its florets, an important indication of seed ripeness . . .). In the sunflower the outer, or ray-florets, are larger and more conspicuous than the inner, owing to an enormous extension of the petals on the outer side of the floret. These ray florets are pistillate, having a pistil but no stamens, while the central or disc florets are hermaphrodite. The inferior ovary contains one ovule (attached to the base of the chamber), which ripens to form a dry one-seeded fruit, the seed being filled with the straight embryo.

The flower-heads of the sunflower are a perfect example of an adaptation for insect pollination as the crowding of the flowers ensures conspicuousness and the pollination of a maximum number of flowers by a single insect visit. The honey, secreted at the base of the style, is protected by the corolla tube from visits of short-tongued insects (which may be why even bumble bees seem sometimes to visit sunflower more readily than hive bees, the former having a longer proboscis). When the flower opens the receptive surfaces of the two stigmas are pressed together and occupy a position at the base of the tube formed by the united anthers; the latter split on the inside and the liberated pollen fills the cavity of the tube and exposes it to contact with visiting insects; finally the style protrudes right through the anther tube and the stigmas spread apart and expose their formerly hidden receptive surfaces. Thus the life history of the flower falls into two stages, the first male and the second female. This favours cross-pollination as compared with self-pollination.

According to Heiser (1976) the style spreads apart to expose the stigmatic surface and the floral mechanism doesn't prevent cross pollination of the flowers in the same head or on the same plant. Also see discussion of the flower process by Putt (1940).

Free and Simpson (1964:341) emphasize that "sunflower heads [presumably the monocephalic domesticated sunflower] isolated from insects set little or no seed, indicating that the florets are usually self-sterile. Cross-pollination by insects between heads of different plants resulted in a greater seed set than pollination between florets on the same head." They add that

in sunflower floret the receptive lobes of the stigma are not exposed until the day after pollen presentation, thus discouraging pollination of a floret by its own pollen. However, toward the end of flowering the stigmatic lobes curl downwards and may touch pollen adhering to the style, and according to Hurt and Furgala a floret may sometimes be fertilized with its own pollen when it has failed to receive pollen from another. Several workers found that sunflower

heads enclosed in paper or muslin bags produce fewer seeds than those exposed to insect visits, but it was not known whether a stigma needs pollen from another plant, or merely from another floret on the same flower or plant, for fertilization to occur, although circumstantial evidence indicated that the former was favoured.

Heiser (1965) states that among the 12 species of annual sunflowers, all of which are diploid, self-compatibility is rather rare. Self-compatibility, however, is known in many of the cultivars of the commercial sunflower. He adds that all of the widespread species of annual sunflowers are self-incompatible. The perennial sunflowers are mostly diploids and are also self-incompatible (Heiser, 1961). Thus the importance of pollinators is clear in the maintenance of species, in hybridization, and the presumed introgression that has been used to explain much of the evolution in groups of closely related species.

EXTRA-FLORAL NECTARIES.—Free (1970:33–34) comments that

many crop plants (e.g. *Vicia faba*, *Ricinus communis*, *Helianthus annuus*, *Cannabis sativus* and *Gossypium* spp.) have extra-floral nectaries. [For a more complete list of taxonomic distribution of floral nectaries see Bentley (1977).] Although they undoubtedly served some useful biological function in their place of origin (see Ruppolt, 1961), they seem sometimes to have a detrimental effect on pollination, especially when they secrete nectar before the flowers open because bees that become conditioned to them do not visit the flowers and so do not pollinate.

Faegri and van der Pijl (1966:54–55), in their analysis of the role of such nectaries state:

Obviously, the easily available sugar of extra-nuptial nectaries is much sought after by sugar-consuming animals, especially in the Tropics extra-nuptial nectar (Zimmermann, 1932) forms an important part of the diet of many insects, for example primitive hymenoptera. There is a whole complex of utilization of this nectar parallel to, but independent of and slightly different from the utilization of floral nectar. Many typical blossom visitors also visit extra-nuptial nectaries (Knoll, 1926), and negative observations (e.g. Springensgut, 1935) may be due to the fact that plants have been studied outside their natural region, as well as to an erroneous primary conception of the function of these nectaries. Utilization of extra-nuptial nectar seems, on the whole to be without primary ecological significance for the plant but more like an innocuous parasitic behaviour.

However, even if nectar and nectaries are thus possibly phylogenetically older than pollination, and even if floral

nectar production and its attendant ecological function only represent the utilization of an already existing mechanism, there is no doubt that nectar production acquired a new aspect as the need for floral attractant of this type arose, and the occurrence, variability and productivity of floral nectaries far outweigh those of extra-floral ones. The occurrence of extra-floral, but nuptial nectaries (i.e. nectaries occurring outside the flowers, but playing a role in the visit of animals to the blossoms), is also more easily understood on this assumption. In the cyathia of Euphorbiaceae they are especially well-developed and form the only attractant produced—as such—by those blossoms. In *Poinsettia* they are so big and productive that they are even utilized by birds.

The extra-floral nectaries in *H. annuus* are located at the edges of the bracts and on the upper leaves. Bagnoli (1975) working in Italy found that about 10 percent of the honeybees visiting commercial sunflowers worked exclusively on extra-floral nectaries (see page 20).

GEOGRAPHICAL DISTRIBUTION.—Heiser (1949; Heiser et al., 1969) has summarized the distribution of the common sunflower, *Helianthus annuus*. He reports that it occurs as a weed throughout the greater part of the United States and adjacent parts of Canada and Mexico, and that domesticated forms of it are cultivated throughout most of the world. He adds that the species is extremely variable and that although part of the observed variation is due to ecological modification of the phenotype, a great deal of true diversity exists within the species.

According to Heiser (1949:157),

the wide distribution of *H. annuus* in the United States is probably a direct result of its weedy tendencies and its introduction by man into many regions. It is extremely doubtful if the species occurs in any area undisturbed by man. In many parts of the Middle West and occasionally in the eastern United States, the sunflower is found in railroad yards, about waste places, and to a lesser extent along roadsides. Throughout most of the western United States the sunflower is particularly common along roadsides and railroad rights of way. The race occurring in the western United States is in general much smaller than the eastern race and has fewer rays, a smaller disk, and leaves which may be truncate rather than cordate. The two races appear to intergrade freely in many regions and it is difficult to determine to which form a single herbarium specimen should be referred. However, when whole populations are examined or when the two forms are grown together in the experimental garden the differences are frequently striking. Both races occasionally may cross with the cultivated sunflower.

Hybridization with other species of annual sunflowers resulting in introgression has greatly increased the variability of this species. Reciprocal introgression between *H. annuus* and *H. petiolaris* is known to occur (Heiser, 1947) and, judging from circumstantial evidence, hybridization between *H. annuus* and *H. debilis* var. *cucumerifolius* in Texas also takes place. A successful cross between these two species has been reported by Cockerell (1915a) and has also been made by the writer.

As to California, Heiser (1949:158) concludes that in all probability *H. annuus* was not introduced into California until fairly recently. He reports that the early botanists in the state did not consider it indigenous and it may well have been introduced by Indians. He emphasizes that sunflower seeds were an important item in the diet of many Indians, and moreover, the "flowers" often had ceremonial usage.

VARIATION AND SUBSPECIATION.—Heiser (1954; Heiser et al., 1969) has discussed variation and subspeciation in *H. annuus*. As he has pointed out, it is a widely distributed and highly variable species comprising both cultivated and wild or weedy forms. Primarily through the culture of plants from many different areas in the experimental garden, variation of certain characters has been studied; thus purple anther color is found throughout the entire range of the species, red anther color is seen in plants from the west, black anther color is found in the cultivated sunflower and occasionally in plants in nature from the central and eastern United States.

He emphasizes that great variation is found to exist in ray number and disk diameter; plants with small disks and few rays occur in the west and Texas, whereas the more eastwardly plants have more numerous rays and larger disks. The achene length is quite variable in the west and east, although the plants from Texas are found to have the smallest achenes and there is a tendency for the eastern plants to have larger achenes. Certain exceptional western populations have been grown that have large heads and achenes, numerous rays, and occasionally black anthers; he suggests that they have arisen through hybridization of the native sunflowers of the region with the cultivated sunflower.

He states that there is also some evidence of

hybridization of the cultivated sunflowers with the wild "races" in the east. Three subspecies, *lenticularis*, *texanus*, and *annuus*, and one variety, *macrocarpus*, were formally recognized and described by him (Heiser, 1954), but later (Heiser et al., 1969) he abandoned their formal recognition as subspecies. Some speculation is entertained in regard to the relationships of *H. annuus* and the origin of its subspecies. Heiser (1954) has concluded that the subspecies *lenticularis* is probably the most similar to the original form of the species, and that subspecies *annuus* arose from *lenticularis* and in turn gave rise to the variety *macrocarpus*. Subspecies *texanus* is thought to have arisen as the result of the introduction of either *lenticularis* or *annuus* into Texas with the subsequent introgression of genes from *H. debilis* var. *cucumerifolius*. Heiser regards it as probable that the complicated variation pattern exhibited by *H. annuus* can be explained largely by the weedy nature of the species and the extensive hybridization within the species and with the other annual sunflowers.

HABITATS OF WILD POPULATIONS OF *Helianthus annuus*.—While travelling through the Southwest seeking sampling sites for bees from *Helianthus annuus*, we found that its habitat preferences were abundantly clear. The plants tended to grow as dense weeds on disturbed land, particularly where moisture was available, as along irrigation and drainage ditches and road and highway shoulders. Many of the best and most accessible sites were recently abandoned fields in agricultural areas on the periphery of small towns. In such cases it was not uncommon to find sunflowers growing in dense stands in one or more portions of abandoned fields during the first year of non-cultivation. That this may be a widespread characteristic of the species is suggested by the studies of Booth (1941) and Wilson and Rice (1968) in abandoned fields in central Oklahoma and southeastern Kansas where *H. annuus* is the first stage dominant in old-field succession. They found that this stage characteristically lasted only two or three years. Wilson and Rice (1968) demonstrated that this dominance and its short duration were due not to successful competition but to allelo-

pathy and resulted from the production of chemical inhibitors to plant growth. The inhibitors affected not only potential plant competitors but sunflower seedlings as well, thus explaining the short duration of the period of dominance.

In any event, the highly mobile *Helianthus*-visiting bees, especially the oligoleges and regular polyleges, quickly find the newly appearing plants and in no instance in our experience did we fail to find some species of bees present during the appropriate season under weather conditions conducive to flight.

ANTHESIS.—In our sampling of sunflower bees, we have noticed a considerable amount of variation in the diurnal cycle of pollen release in wild populations of *Helianthus annuus*. The factors influencing these variations were not investigated in detail but the most obvious as they affect initial anthesis in the morning are temperature and sunlight. On a cool morning after sunrise the bees will frequently arrive at the flower heads before the male florets have released pollen although nectar is available at that time. On other occasions we have observed anthesis taking place at or before sunrise. When the sky is cloudy in the east or the sky overcast, anthesis may be delayed for an hour or more and this is reflected in reduced bee activity.

Some wild populations of *H. annuus* apparently make pollen available more than once during the day and this is reflected in the size of the pollen loads carried by the bees. In other populations anthesis apparently takes place all at once with large quantities of pollen released early in the morning and when bees are abundant it is essentially removed by the bees before noon.

HYBRID SUNFLOWERS.—Hybridization among annual sunflowers occurring in nature, especially hybrids with the common sunflower *Helianthus annuus*, have been known for a number of years (see, for example, Cockerell, 1929), but have only recently been given serious analytical attention in terms of evolution and speciation by Heiser (1947, 1949, 1951a, 1951b, 1954, 1955, 1961, 1965; Heiser et al., 1969, etc., to cite a few of his important contributions to this field). More recently, however, attention has been given to im-

proving the quality of commercial varieties of *Helianthus*, and hybrids are now being made available in various parts of the United States that are claimed to be superior to open-pollinated varieties (Anon., 1975a, 1975b). Nearly all of the hybrid sunflowers now grown in the United States result from use of cytoplasmic male sterility discovered by Leclercq (1970; Heiser, 1976). Hybridization also occurs among perennial sunflowers (Long, 1955, 1959, 1960).

HORTICULTURAL (ORNAMENTAL) VARIETIES.—The single-headed commercial variety of *Helianthus annuus* has long been utilized for ornamental purposes as a garden plant, and in recent years has been strongly recommended by groups interested in “organic gardening” as a home grown garden crop (Anon., 1961; Brinhardt, 1961).

Heiser (Heiser et al., 1969:32) states that

in addition to *H. annuus*, several other species have ornamental value and are occasionally seen in gardens. The principal species employed are the two annuals: *H. argophyllus* (the silvery-leaved sunflower), *H. debilis* ssp. *cucumerifolius* (the cucumber-leaf sunflower), and several perennials: *H. maximiliani*, *H. mollis*, *H. rigidus*, *H. salicifolius* (the willow-leaved sunflower), and the hybrids, *H. laetiflorus* and *H. x multiflorus*.

And later, with reference in particular to *H. annuus* he comments (page 66) that the annual ornamentals

differ from the wild sunflowers chiefly in the number or the color of the rays—primrose, chestnut, plum—and their sometimes larger disk and achenes. The red-rayed forms are apparently all derived from a mutant plant found in the wild in Colorado by Mrs. T.D.A. Cockerell (Cockerell, 1912, 1918). The “double-flowered” forms probably originated in Europe shortly after the introduction of the sunflower there. Cockerell (see Watson, 1929:361) has given formal taxonomic recognition to many of the ornamental variants, but there seems little to be gained by trying to designate the various ornamental forms with Latin names.

Since the red sunflower was discovered by the wife of the eminent naturalist and distinguished Melittologist, T.D.A. Cockerell (see W. P. Cockerell, 1941, as well as T.D.A. Cockerell, 1912, 1918), the following quote from T.D.A. Cockerell (1938:117) seems appropriate.

In the summer of 1910, at Boulder, Colorado, my wife discovered a red sunflower growing by the roadside close to our house. It was a wild plant, one of a group of prairie

sunflowers, *Helianthus annuus lenticularis*, a plant which is excessively common in this locality, growing especially in soil which has been disturbed. This form has comparatively small heads, bright orange rays, and nearly black discs. The dark color of the disc is due to an anthocyanin pigment dissolved in the sap, a pigment which is also found in many related plants. The new mutation was a plant in which this pigment had increased so that it invaded the rays, and produced a chestnut-red coloration in combination with the orange plastids already present. When we think of the red in the rays of the *Gaillardia* and other composites, this does not seem surprising; but in the genus *Helianthus* it was a new break, evidently of horticultural value. We dug the plant up with great care, and transferred it to our garden, where it continued to bloom. It was well that we did so, for a few days later a city official mowed down all the "weeds" in that row. This one plant, thus found and preserved, was the ancestor of all the red-rayed *Helianthus annuus* which are now well known in floriculture, in many parts of the world.

The perennial Jerusalem Artichoke, *Helianthus tuberosus*, normally grown for its edible tubers, is also grown as an ornamental plant in California (Anon., 1974).

COMMERCIAL SUNFLOWERS.—As Heiser (1951c:432) comments,

the origin of cultivated plants has long challenged the imagination of both botanists and anthropologists. The problems relating to the tracing of such origins have been subject to renewed interest and scientific inquiry in recent years. The cultivated sunflower thus far has received relatively little attention in such studies, but it is of particular interest because it is one of the few crop plants to have been domesticated in temperate North America and it is one of the few plants whose wild progenitor still exists.

Hurt (1948:47) states that

the commercial sunflower of today is believed to have originated in Peru or Mexico, whence it was first introduced into Europe by the Spaniards in the sixteenth century. After its introduction to Spain, it spread to Bavaria in 1625, to France in 1787, and then to Hungary, Russia and other parts of Europe. Sunflower was reintroduced into the Argentine, as a commercial crop, in 1870.

Heiser (1976), however, does not find evidence that the commercial sunflower originated in Peru or Mexico.

According to Hurt (1948:47), "the Anglo-Saxon term was 'Solsacce,' the Spaniards calling them 'Girasol' and the French 'Tournesol.' All these terms imply 'turning with the sun' and seem to have been due to a rather imaginary belief

that the flower turned with the sun. . . . Actually, however, the word sunflower is much more likely to originate from the resemblance of the flower to rays of the sun." For a more extensive discussion of the origin of these terms see Salaman (1940) and Heiser (1976).

With regard to the sunflower's turning with the sun, Shinnors (1956:88) remarks:

Contrary to Blake's famous poem, the heads during the summer face away from the sun, not toward it, even at times when the prevailing southerly winds are not strong enough to tip them northward. Purposeful or not, this behavior means that the open florets are partly shaded and (doubtless aided by evaporation from the enormous surface area exposed by the many individual flowers in the head) relatively cool. On the driest and hottest days of summer, individuals of the very common bee *Diadasia enavata* and one or two species of usually alert and swift *Melissodes* can be found resting sluggishly on the disk at the base of the ray florets. In windy weather, the rays (which produce no pollen) clearly serve as a partial windbreak, making it easier for flying insects to approach and land on the disk. Thus the structure of the sunflower head not only assists visitors to alight, but in addition shelters them against extremes of sun and wind, insuring the survival of a supply of pollinators for milder times.

Heiser (1951c:432), in his discussion of the sunflower among American Indians, emphasizes that "the common sunflower, *Helianthus annuus* L., comprises three varieties: *H. annuus* var. *lenticularis* (Dougl.) Ckll., the 'wild' sunflower; *H. annuus* var. *annuus*, the 'weed' or 'ruderal' sunflower; and *H. annuus* var. *macrocarpus* (D.C.) Ckll., the giant sunflower which is cultivated for its edible seeds."

In 1955 Heiser summarized his views on the origin of the cultivated sunflower as follows (page 166):

From evidence now at hand it is clear that the sunflower was domesticated in temperate North America. It is not possible to reconstruct the definite steps leading to the origin of this plant but the following working hypothesis may be advanced. The wild sunflower (*H. annuus* ssp. *lenticularis*) in remote times became a food plant of the Indians of western North America. In time it became a camp-following weed and was carried into many new areas by the Indians. In the central and eastern United States the new weed became more or less stabilized and the race known as *H. annuus* ssp. *annuus* had its origin. This weed may actually have been brought into cultivation and with the selection of mutants restricting branching and increasing seed size this plant

could have developed into the giant, monocephalic plant known today as *H. annuus* var. *macrocarpus*. It is not possible to point to one definite region as the center of origin of the new form but the present distribution of the weed sunflower and the distribution of the archaeological sunflowers strongly suggest the central United States as the place of origin.

The sunflower, then, is unique in having its origin in temperate North America, for the majority of American food plants were brought into domestication in Central or South America. Whether the sunflower was domesticated before these Indians had acquired other cultigens and thus agriculture had an independent origin in temperate North America or whether the sunflower was brought into cultivation after these Indians had acquired the knowledge of agriculture from other peoples is not clear. It may have been that the sunflower was a basic food before the introduction of maize. With the introduction of maize, a most superior food plant, the sunflower lost its dominant position and was kept mainly for its secondary uses as a dye and oil plant. However, as yet there are not enough facts to allow much more than speculation on this interesting subject.

Although the sunflower has long been grown as an oil crop abroad, especially in Russia where varieties with seeds of high oil content have been given special attention, only recently has oil seed production in the United States begun to assume major importance (Posey, 1969; McGregor, 1976). Russian cultivars, however, have been grown and developed along with new oil producing varieties since shortly after World War II. Originally much of the U.S. production was grown for silage (Atkinson, 1919; Cardon, 1922; Kucinsky and Eisenmenger, 1944) and still is (Gage, 1963), as well as for consumption as seed by birds and humans. More recently, the dehulled kernels have been roasted and sold as a confection.

Sunflower oil is useful for salad and cooking oils, shortening, and margarine due to its stable qualities and high ratio of polyunsaturated fatty acids (Anderson, 1970; Trotter, 1970) and sunflower meal has a number of potential uses (Talley, Brummett, and Burns, 1970). It is also a desirable ingredient in paints because of its low linolenic acid content (Anderson, 1970) and is used as an industrial lubricant (McGregor, 1976). North and South Dakota and Minnesota are the major oil producers in the United States with a million acres of sunflowers, three-fourths of them in the Red River Valley (Anon., 1975b).

Throughout the world more than 17 million acres are grown annually in more than 50 countries (Burns, 1965).

According to Hurt (1948) there are some 50 cultivated varieties of *H. annuus* chiefly distinguished by height or by the color of their seed.

INSECTS INJURIOUS TO SUNFLOWERS.—It is not our object to review the status of insect pests of commercial sunflowers, even in North America, since they are mostly highly regionalized and many have been inadequately studied and evaluated from the economic and ecological viewpoint. Actually, the literature on sunflower pests is more extensive abroad, where, until recently, the plants have received more attention as seed and oil crops than in their native America.

Rajamokan (1976) has tabulated the reported sunflower pests of the world, the part of the plant attacked, the importance of the pests to the extent known at the time of publication, and provided a bibliography of published papers on the subject. Almost all such pests are endemic to the areas where commercial sunflowers are grown, either as native or introduced crops. Even in general textbooks emphasizing economic entomology in North America, the importance of sunflower insects has varied. We cite only Essig (1926), who lists 28 species of insects feeding upon wild and cultivated sunflower in the west, including tetranychid mites, thrips, membracids, leafhoppers, aphids, coccids, mealybugs, pentatomids, scarabs, chrysomelids, tephritids, agromyzids, nymphalids, arctiids, noctuids, and tortricids, and Metcalf and Flint (1962), who record only three sunflower pests.

In the course of our search of the North American literature for records of sunflower bees we have encountered a number of papers on commercial sunflower pests that cite other species of *Helianthus*, especially the wild *H. annuus* as alternate hosts, as would be expected, and other related Compositae (see, for example, Satherwait, 1946, 1948; Schulz, 1973; Teetes and Randolph, 1969; Westdal and Barrett, 1955).

To our knowledge, the first attempt to treat the general entomology of *Helianthus* was that of Cockerell (1914d), whose examples, in addition

to those from abroad, included more precise data from the western United States, primarily Colorado and New Mexico. The most complete regional list of sunflower insects is that of Walker (1936) on the sunflower insects of Kansas. Other regional lists are provided by Adams and Gaines (1950), Beckham and Tippins (1972), Breland (1938, 1939), Phillips, Randolph, and Teetes (1973), Satherwait (1946, 1948), Satherwait and Swain (1946), and Seiss (1897). The most complete treatment of sunflower insects in North America is by Schulz (1978).

Since sunflower seeds are a preferred bird food, it is not surprising that many species of birds damage sunflowers. For a discussion of the most important species, factors affecting loss, and means of crop protection see Besser (1978).

Among the sunflower pests in the southwest, perhaps the most widespread are the sunflower moth, *Homoeosoma electellum* (Hulst) and the root feeding scarab, *Bothynus gibbosus* (DeGeer). Knowles and Lange (1954) and Carlson (1968) discuss the sunflower moth in California where it is not only the most important pest of commercial sunflower but also attacks wild sunflower and certain cultivated Compositae. They illustrate damage to flower heads and seeds, webbing and larval frass. Carlson briefly describes its habits and seasonal occurrence in that state and also illustrates the larva. More recently, Rogers (1978) has discussed the feeding behavior of the larva and Carlson et al. (1978) have investigated the flight activity of this moth. The most complete studies of this pest, however, have been made in Texas by Teetes and colleagues (Teetes and Randolph, 1969, 1970a, 1970b, and Randolph, Teetes, and Baxter, 1972). The muck or carrot beetle, *Bothynus gibbosus*, mentioned in many publications relating to sunflower pests of the South and Southwest, has been treated most thoroughly by Botrell and Brigham (1970).

Rogers (1977a) has recently published an account of the lace bug *Corythuca morelli* Osborn and Drake as a pest of sunflower in the southwest (Texas) as well as an account of cerambycid pests of sunflowers in the Southern Plains (Rogers, 1977b, see also Muma et al., 1950). Baerg (1921)

has described injury to Jerusalem artichokes (*Helianthus tuberosus*) by a cerambycid girdler (*Mecas* sp.) growing in Arkansas. Rogers, Thompson, and Stoetzel (1978) have presented information about the distribution and hosts of the Aphidae of sunflowers in North America and Rogers, Thompson, and Gagné (1979) have developed similar data for the Cecidomyiidae. Resistance in wild *Helianthus* to the sunflower beetle, *Zygotogramma exclamationis* (Fabricius), has been described by Rogers and Thompson (1978). In Manitoba, Westdal and Barrett (1960, 1962) have concluded that the trypetid *Strauzia longipennis*, although abundant and destroying the stem pith, is not an economic pest.

It is not surprising that new sunflower pests are still being discovered and will no doubt continue to be so. Schulz (1973) has described and illustrated damage to the heads of commercial sunflowers by the recently discovered (Gagné, 1972), cecidomyiid *Contarinia schulzi*, which severely infested 10 percent of the total acreage planted to sunflower in North Dakota and Minnesota in 1971. The species has also been collected from the wild sunflowers *Helianthus annuus*, *H. petiolaris*, and *H. maximiliani*.

Intrafloral Relationships of Bees Associated with *Helianthus*

All species of *Helianthus* in North America, with one principal exception, are obligate outcrossers since the flowers are self-incompatible. Also, insofar as known, all the species produce copious amounts of both nectar and pollen and, therefore, it is not surprising to find that the flowers are visited by a wide variety of anthophilous insects, especially native bees. Further, since the pollen readily clings to the body hairs and appendages of these various visitors, there is no reason to doubt that it is transported to other flowers and is thus available to effect pollination if it comes into contact with a receptive stigma. Among the insect visitors, however, with few exceptions, only the native bees have established significant intrafloral relationships with these flowers.

ENDEMIC BEE VISITORS TO *Helianthus* ABROAD.—The literature of eastern Europe and the Soviet

Union contains many references to bee visitors to the introduced *Helianthus annuus* under the names of various commercial varieties. It is beyond the scope of this paper to summarize these but it may be of interest to note that as early as 1913 Alfken, in Bremen, recorded eight species of *Bombus*, three species of *Psithyrus*, two species of *Megachile*, one species each of *Halictus*, *Coelioxys*, and *Anthidium*, and *Apis mellifera* visiting cultivated *Helianthus annuus*. Recently Bagnoli (1975) in Italy discussed the importance of various species of native Apoidea along with certain other insects, including Coleoptera and Hemiptera, as pollinators of commercial sunflowers. With regard to the bees, he noted that fields separated by only a few tens of kilometers exhibited large differences in their density. At one locality there were numerous *Ceratina* spp., in other *Halictus* spp. and *Andrena* spp., and at a third, 60–70 percent of all the Apoidea were *Bombus terrestris* L. and *B. lapidarius* L.

Cockerell (1914b) commented that the perennial sunflowers in European gardens are visited by *Bombus*, *Psithyrus*, *Halictus*, *Megachile*, and *Heriades*. He added that in Australia, *H. annuus* is freely visited by *Trigona carbonaria* collecting pollen, while in New Zealand, in the absence of native long-tongued Apoidea, the only bee visitors are the introduced species of *Bombus* and *Apis*.

Kapil, Chaudhary, and Jain (1975) reported that a preliminary survey of insect pollinators of sunflower in Hisoar, India, during August–September 1974, showed that the flowers of this crop were visited by *Xylocopa fenestrata* (Fabricius), *Xylocopa pubescens* Spinola, *Megachile lanata* (Fabricius), two unidentified *Megachile* spp., *Nomia* sp., *Melissodes* sp., *Braunsapis* sp., and *Apis florea* Fabricius. During April 1975, however, the flowers of this crop were visited by only four pollinators, namely an unidentified *Megachile* sp., *X. fenestrata*, *Braunsapis* sp., and *A. florea*. Among them the population of *Braunsapis* sp. was maximum, varying from 17 to 50 bees per 500 flowers during the second and third weeks of April.

With the exception of *Braunsapis*, these combinations of genera, both in Europe and India, are not much different from those that might be found in North America where *Helianthus* was

either not endemic or not long established. Yet, to judge from books on the subject, one would be led to believe that the only important pollinators of sunflower are honeybees not only in those areas of the world where the sunflower is introduced, but also in the United States where it is native. Surely, where honeybees are available and are attracted to sunflowers there can be no doubt as to their importance as pollinators, where autogamy, cross-pollination, or outcrossing are desirable features in ornamental, commercial, or wild species. The role of other bees, however, also deserves attention and their potential should not be ignored.

Although wild sunflowers clearly provide a reservoir for pollination of ornamental and commercial sunflowers, they also provide a source of genetic contamination in inbred lines used for production of planting seed. Schacht (1979), an experienced farm reporter in California, had this to say about sunflower seed production in that state:

A few weeks ago I remarked here that California growers had been left out of the national boom in planting of sunflowers to produce "sun oil."

True, but as Benjamin H. Beard, research geneticist in oilseed production at University of California-Davis, has been quick to inform me, they are taking part in this development in a different way. They are raising the seed which the farmers in states like North Dakota and Minnesota are planting.

According to Beard, perhaps 25 percent of all the seed of sunflower varieties raised for oil production is now harvested from California fields. As is so often the case, our climate and growing conditions make a specialized farming deal possible.

Beard says that "we have some unique conditions in California which allow farmers to grow high quality sunflower seed. Seed is produced from highly selected inbred lines. Six to ten rows of female plants are planted with two or more rows of male pollen-producing plants. Bees transfer the pollen from the male to the female plants. Only the female rows are harvested. This seed is planted commercially and the resulting plants are true hybrids which as in the case of hybrid corn produce more seed than the older open-pollinated varieties."

An area stretching north from Dixon along the western side of the Sacramento Valley has proved particularly well suited to raising sunflower seed. For one thing, according to Beard, none of the major diseases of sunflowers are normally found there. A second and very important plus is that it

seldom rains there during the growing season and this "assures clean bright seed." Plenty of irrigation water is available so the plants need not suffer while they are developing their seed crop.

Just as important is the fact that the seed fields are isolated from contamination by unwanted varieties. Beard explains: "Another major factor is that there are only a few wild sunflowers there. In order to produce a uniform commercial crop the pollen must all come from the selected male inbred plant. Thus one requirement for hybrid sunflower seed production is that the field must be at least two miles minimum from other pollen-producing sunflowers."

Concludes Beard: "So while California farmers are not producing much sunflower oil they are a necessary part of the sunflower oil boom."

INTRODUCED HONEYBEE AND SUNFLOWER POLLINATION.—Cockerell (1914c) reported on a census of bees visiting cultivated sunflowers at Goodview, Colorado, and found the honeybee to be an insignificant factor in sunflower pollination. He was also informed by a beekeeper in Boulder that honeybees do not go to sunflowers unless the supply of other nectar runs short and that when they do make honey from sunflowers it is very yellow. Bees visiting commercial sunflowers at Goodview were *Andrena helianthi*, *Halictus armaticeps*, *Dufourea marginata*, *Pseudopanurgus innuptus*, *Melissodes aurigena* (= *M. agilis*), *M. confusiformis* (= *M. coreopsis*), and *Megachile agustini*.

Robertson (1929) in a cumulative survey of insects visiting cultivated sunflowers at Carlinville, Illinois, presumably growing in his yard, between the dates of 11 July and 6 September, collected 42 species, of which 28 were bees as follows (nomenclature updated): *Andrena accepta*, 1♀; *A. helianthi*, 1♂; *Apis mellifera*, 65♀NP; *Augochloropsis m. metallica*, 11♂♀; *Bombus bimaculatus*, 5♂; *B. griseocollis*, 12♂; *B. impatiens*, 26♂♀NP; *B. p. pennsylvanicus*, 5♀NP; *B. v. vagans*, 2♀; *Ceratina dupla*, 1♀NP; *Dialictus imitatus*, 1♀P; *D. p. pilosus*, 1♀P; *D. versatus*, 1♀P; *Halictus c. confusus*, 1♀; *H. ligatus*, 50♂♀P; *Megachile brevis*, 1♀; *M. inimica*, 1♀; *M. mendica*, 1♀NP; *Melissodes agilis*, 50♂♀NP; *M. bimaculata*, 1♂, 1♀; *M. boltoniae*, 6♂♀NP; *M. coloradensis*, 2♀NP; *M. dentiventris*, 1♀; *M. trinodis*, 4♂♀NP; *Psithyrus variabilis*, 8♂♀; *Svastra obliqua*, 6♂♀NP; *Triepeolus concavus*, 1♀.

Guynn and Jaycox (1973) made some obser-

vations on sunflower pollination in Illinois after moving 15 two-story hives of honeybees to a 15-acre commercial planting. Their experiments confirmed that sunflowers require insect pollination. The honeybees, however, did not collect and store much of the sunflower pollen, preferring to clean it off in the field, where much of it dropped onto leaves near the flower heads. The experimental colonies produced a golden-colored honey with a pleasing, mild flavor. Counts of honeybees at the sunflowers were relatively low and were not correlated with yields. Many other insects were observed but not accurately identified or counted. Commercial beekeepers had variable results in honey production from sunflowers, perhaps because of unfavorable weather. Their general conclusion, however, was that lack of competing nectar plants during sunflower bloom and the presence of other pollinators probably combined to bring available insects to the fields and helped to produce a respectable seed yield throughout the state.

In the most recent publication on the subject by an American author, McGregor (1976:349) summarizes the situation as follows:

All research on sunflower pollination indicates that honeybees are the primary pollinating agents, and that colonies should be provided to the field (Barbier and Abid 1966), and that they should be protected from harmful pesticides while they are in the field. The bees should be ready for the pollination task at the onset of flowering. The total flowering period is usually about 20 days, but 83 percent of the heads begin to open within 3 days after the first head opens. Evidence also indicates that the highest bee population and the highest production occur within a few hundred feet of the apiary. If adequate pollination throughout the field is provided, there should be no significant gradient of seed set in relation to apiary location.

The term "saturation pollination," meaning the patterned distribution of groups of colonies, sometimes used on other crops to provide adequate coverage throughout the entire field, is equally applicable and needed in sunflower production.

After quoting different recommendations of the number of colonies per hectare or per acre required for sunflower pollination he comments that "the evidence is plain that, if the grower wants maximum seed production, he should not skimp on the use of bees."

He adds that

the number of colonies per acre alone is not too meaningful. Distribution of colonies to give thorough coverage of all blooms is highly important, and strength and other conditions of the colony are equally important. The criterion the grower should use is the bee visits per floret or bees per head throughout his field. The presence of one bee per head throughout the day should provide adequate visitation, but additional research is needed to determine the exact bee population needed for maximum production of sunflower seed.

As might be expected, most of the studies on the role of honeybees in the pollination of the commercial varieties of *Helianthus annuus* are from those parts of the world where sunflower is an introduced crop, particularly from the U.S.S.R., eastern Europe, and from France, England, and India, for example, see Avetisyan (1965), Baculinski (1957), Cirnu (1960), Free (1964), Katarov (1971), Kurennoi (1957), Kushnir (1960), Radaeva (1954), Radoev (1954), Rangarajan, Mahadevan, and Iyemperumal (1974), Rozov (1933), Schelotto and Pereyras (1971).

Summarizing the results of observations and experiments with honeybees as pollinators of the sunflower in various zones of the U.S.S.R., Rozov (1933:305) states that

bees visit the flowers chiefly for the purpose of collecting nectar. The flowers in the antheral stage of florescence, as secreting more nectar, are visited by bees 3-5 times as often as in the stigmatic stage of florescence. In order to secure a complete pollination, the flowers must be visited by bees no less than ten times on an average.

Experiments conducted on fields sown with sunflower show that bees not only can replace wild pollen carriers but also increase the pollination and the fertilization of ovules considerably (no less than 25-30%). The role of bees as pollen carriers is more conspicuous when the plants are in good condition, since in that case they secrete a greater amount of nectar and thereby attract bees to a greater degree, on the one hand, and, on the other hand, they can provide for the development of a greater percentage of achenes.

... Large areas sown with sunflower must be provided with apiaries for pollinating purposes. The bees of such apiaries not only will replace wild pollen carriers, but, owing to their pollinating activity, will considerably increase the fertilization of ovules and, hence, the yield of sunflower seed. Moreover, such apiaries will pay well in honey.

Mel'nichenko (1976) has summarized the role of insects and the honeybee in increasing the yield of agricultural plants, including *Helianthus*, in Russia.

According to Free (1964), honeybees visiting sunflowers collect food from only a small proportion of florets per flower head. He states (1966) that pollen gatherers restrict their visits to florets in the male stage and only nectar-gatherers touch the female stage florets and pollinate them and also (1970:73) that since "nectar gatherers are the more valuable pollinators of *Helianthus annuus* which presents its pollen in the morning ... for this crop it might be advantageous to delay releasing colonies until the peak of pollen presentation is finished for the day."

Bagnoli (1975), in Italy, confirms that nectar-gathering honeybees are the most efficient pollinators; that when dusted with pollen while exploiting the nectar in the anther tube, the bee does lodge pollen in the corbiculae but almost totally discards the rest as it leaves the flower. He found that about 10 percent of the bees worked exclusively on extra-floral nectaries situated at the edges of bracts and the foliar laminae. He regards it as probable that the secretory organs of these cells begin activity shortly before the opening of the inflorescence in order to attract the attention of pollinating insects at the right moment. Although work in Italy demonstrates the importance of honeybees in sunflower pollination, it also reveals the useful role of native bees (see "Native Bee-Flower Relationships in North America," immediately following).

Palmer-Jones and Forster' (1975) have made some observations on sunflower pollination in New Zealand where the plant is being grown on an increasing scale, mainly as an oil crop. They note that few bees were seen carrying pollen in their corbiculae but that when forced to collect sunflower pollen, as in cages, they had no difficulty in gathering it. They found that bees from hives within range consistently collect nectar from the flowers. They conclude that

sunflowers are not fully dependent on honeybees for pollination, as a low yield of seeds, with a germination rate of

99%, formed in the cage that excluded bees. Crops with low bee coverage also yielded good quality seed, but yield was lower than when bee coverage was high. The number of plump seeds produced per head is considered to provide a reasonably accurate measure of the degree of pollination (1975:97).

In the desert valley areas of southern California, Lehman et al. (1973) note that sunflowers require honeybees or some other insect for pollination. In their tests, honeybees that were located in hives about a quarter of a mile from a planting and near a good source of water were found to be the main insect pollinators. They remark, however, that fairly high populations of moths, such as the beet army worm and the cabbage looper moth, were present in the May and June plantings, but conclude that the populations of these moths were too variable to be depended upon for good pollination. These investigations recorded honeybee populations during peak bloom on the variety Tchernianka eight times each day for four days at each planting date. They found that honeybee populations of 1.54 bees per flower were highest for the January planting and decreased to a low of about 0.23 bees per flower during the May and July planting. They state that pollination seemed satisfactory at all planting dates.

Furgala (1954, 1970), noting that sunflower ranks among the top four oilseed crops in the world, has proposed "that mission-oriented research in honeybee pollination of sunflowers will directly resolve the central objective of the industry in the United States; namely, how to effectively increase sunflower seed yields" (Furgala, 1970:37).

Our own observations on the behavior of honeybees at sunflowers have been largely limited to the arid southwestern United States where we have generally found them present at low levels or absent (see page 124).

COMPETITION AMONG *Helianthus* FLOWER VISITORS.—In Japan, Kikuchi (1963) studied dominance relationships among insects, especially syrphid flies, blow flies, bees, and bumblebees, visiting flowers of 22 species of plants representing 12 families, about one-third of them Compositae. Various patterns of avoidance behavior were

identified among the insects competing for nectar from almost all of the plant species involved except sunflower (*Helianthus*). Probably Kikuchi was observing the cultivated form of *H. annuus* with the large composite flower head providing a platform with sufficient space and nectaries to minimize antagonism among nectar seekers.

On wild *Helianthus annuus* in the southwest we have seen intense competition between larger bees such as *Bombus* spp., *Suastra* spp., and *Nomia heteropoda*, when excessively abundant, and smaller bees such as the ubiquitous *Melissodes agilis*. This competition is sometimes minimized by early morning and late afternoon pollen collecting by the latter; however, at times they are practically excluded from the plants not only by much larger bees but by the slightly larger, faster, and more aggressive *Diadasia enavata*.

In the central valley of California during the dry period of late summer and fall, the presence of large numbers of syrphid flies—*Eristalis tenax* (L.), *E. stipator* Osten Sacken, and *Eristalis aeneus* Scopoli (det. F. C. Thompson)—and skipper butterflies—particularly males of *Hylephila phylaeus* (Drury) and *Lerodea eufala* (Edwards)—can interfere with pollen- and nectar-seeking by a variety of solitary bees. The presence of *Hylephila phylaeus* is also particularly distracting in the sampling operation because as they alight on the flower with their forewings back to back and their yellowish hind wings spread laterally at a posteriorly directed angle, they bear a striking superficial resemblance to a female bee with heavy loads of *Helianthus* pollen. In southern Arizona bee activity is often markedly reduced by cantharids—*Chauliognathus basalis* LeConte and *C. marginatus* Fabricius (det. Robert D. Gordon)—and mirids—*Adelphocoris superbus* (Uhler)—swarming on the flowerhead and preventing access to the florets.

NATIVE BEE-FLOWER RELATIONSHIPS IN NORTH AMERICA.—Bee-flower relationships reflect various strategies on the part of both sets of participants. For the purpose of the present study we are concerned with the extent and degree to which bees in North America utilize the pollen and nectar of *Helianthus* for their survival as species or for the maintenance of populations depen-

dent at least partly on the pollen or nectar or both of *Helianthus*. We also are concerned with the regularity of this relationship and its bearing on the pollination of *Helianthus*.

The two most commonly recognized behavioral categories with respect to pollen collection by bees are oligolecty and polylecty (see reviews by Grant, 1950, Linsley, 1958, and Baker and Hurd, 1968). Oligolectic bees are generally regarded as those in which all the members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only locally in the face of an absence or shortage of pollen. Polylectic bees are those in which the species as a whole, regardless of the extent to which individual members of the population may exhibit flower constancy in the collection of pollen, are not sharply limited in the number and kind of pollen sources utilized in their economy. Although these categories are by nature relative and not always clearly recognizable, or even definable, they do represent modes in the flower relationships of pollen-collecting bees as a whole (Hurd and Linsley, 1975).

For purposes of the present study these relative categories are further subdivided as follows:

1. Primary oligoleges are those bees that, although oligolectic as a species on Compositae, are primarily associated with *Helianthus*.
2. Secondary oligoleges are those bees that, although oligolectic as a species on Compositae, are secondarily associated with *Helianthus*.
3. Regular polyleges are those bees that, although polylectic as a species (often on Compositae), regularly gather pollen from *Helianthus* where they occur within its range, either as individuals or as populations.
4. Casual polyleges are those bees that, although polylectic as a species, have a preference for the pollens of other plants, but as individuals visit the flowers of *Helianthus* for pollen, usually but not always, in small numbers.

Our data suggest that the evolutionary sequence leading to specific intrafloral relationships by differentiating faunas of bees may have ini-

tially commenced with casual polyleges of the Compositae, some of which evolve into regular polyleges. Later in the sequence some of the regular polyleges evolve into oligoleges of the Compositae, first secondarily associated with *Helianthus* and then ultimately into primary oligoleges which become nearly or entirely dependent upon the pollen, and to a large extent, the nectar of *Helianthus*, including even various subdivisions within that genus. Alternatively, the proposed evolutionary sequence could also proceed from any of the polylege categories (and perhaps even from oligoleges) during periods of environmental stress or prolonged periods of unusual pollen shortages (e.g., *Diadasia enavata*, the only oligolege of the Compositae in genus *Diadasia*).

This investigation reveals that there are at least 284 species of native bees that collect pollen from the flowers of *Helianthus*. Table 3 summarizes by family their relative dependence on the pollen of *Helianthus*.

In addition to these, there are 72 species of pollen-collecting bees that are known to visit the flowers of *Helianthus* for nectar only and 56 species of parasitic bees that also visit the flowers for nectar. Quite obviously the more consistent the relationship between the flower and its pollen vectors, the greater is the degree of pollination. Consequently it is those species of bees which have evolved a specialized intrafloral relationship with *Helianthus* that are the principal pollinators of that plant. Nonetheless, other insects and especially male bees, particularly those of the oligoleges and polyleges mentioned above, often assume important roles in the pollination of these flowers.

Several previous studies have been made of the insect pollinators of *Helianthus*, especially bees. The first such study known to us was made by Cockerell (1898c) who reported on the insect visitors at the flowers of *Helianthus annuus* in New Mexico. Subsequently in several papers, Cockerell (1911, 1914b, 1915b, 1916a, 1917a,b) listed and discussed bees visiting the flowers of *H. annuus* (and at two localities, *H. lenticularis*) in California, Colorado, Connecticut, and Virginia. He also discussed the bee visitors of *Helianthus* growing

TABLE 3.—Relative dependence of native bees on pollen of *Helianthus*

Family	Oligoleges		Polyleges		Totals
	(primary)	(secondary)	(regular)	(casual)	
Colletidae		4		1	5
Oxaeidae					0
Andrenidae	18	32		6	56
Halictidae	4	2	2	38	46
Melittidae	1	1			2
Megachilidae	4	18	8	42	72
Anthophoridae	12	35	6	29	82
Apidae			6	15	21
Totals	39	92	22	131	284

under introduced conditions in the Old World (Cockerell, 1914b, 1916a). Cockerell earlier in collaboration with Swenk (Swenk and Cockerell, 1907a,b and Swenk, 1907) discussed several sunflower-visiting bees from Nebraska. Of these, three species were recorded from *H. petiolaris* and seven species from *H. annuus*.

Graenicher (1909) in his studies of Wisconsin flowers and their pollinators provides information on the bee visitors of *H. giganteus* (12 species) and *H. strumosus* (31 and 38 species from Milwaukee and Cedar Lake, respectively). In a series of papers on the bees of North Dakota, Stevens (1919, 1949a-c, 1950, 1951a-c) presents data on 31 species of bees visiting the flowers of seven species of *Helianthus*, including *H. annuus* (eight species), *H. maximiliani* (12 species), *H. nuttallii* (one species), *H. petiolaris* (21 species), *H. rigidus* (eight species), *H. strumosus* (one species), and *H. tuberosus* (eight species). Robertson (1922) discusses the sunflower and its insect visitors and later, in his volume entitled "Flowers and Insects" (Robertson, 1929), summarizes the information that he had developed on this subject commencing before the turn of the century. In this work he records and provides data for 68 species of bees obtained at the flowers of *Helianthus* growing in the Carlinville area of Illinois including *H. annuus* (25 species), *H. divaricatus* (51 species), *H. grosseserratus* (36 species), *H. mollis* (19 species), *H. rigidus* (17 species), *H. strumosus* (eight species), and *H. tuberosus* (32 species). He also presents information on the bee

visitors of cultivated sunflower (28 species). In a study of the bee-fauna and vegetation of the Miami region of Florida, Graenicher (1930) reports on nine species of bees visiting the flowers of *Helianthus debilis*, an inhabitant of the sand dunes. Michener (1947) in his study of the bees of a limited area in southern Mississippi records sixteen species visiting the flowers of *H. radula*.

In addition to these studies, there is a wealth of floral visitation records pertaining to *Helianthus* in the literature of North American bees. Most of these records are listed in taxonomic publications and we have made a special effort to retrieve this information and incorporate it into the species accounts of this study.

From our studies in North America it seems clear that there are few, if any, oligolectic bees associated solely with *Helianthus*, although there are many oligoleges of Compositae that visit sunflowers for pollen and nectar, as well as others that prefer sunflower pollen, when available, to that of other composites. In the following lists we have tried to classify bee visitors as (1) oligoleges of Compositae primarily associated with sunflower, (2) those secondarily associated with sunflower, and general polyleges, which are either (3) regular or (4) casual visitors. In some cases the data presently available make the decision obvious. When data are limited we have taken the systematics of the bee into account and made an arbitrary assignment which may or may not be confirmed by future collections (for example, we

have been faced with the problem of where to assign species for which the only known flower record for a female is based upon one individual taken at sunflower).

The list of nectar visitors not known to take sunflower pollen is based upon females and males of species whose females do not take sunflower pollen, since males, as well as females, are important pollinators. Obviously, this list will be expanded greatly with future collecting and some species from this list may be shifted to other categories with additional knowledge.

A list of parasitic bees taken at sunflowers is included because, in spite of their reduced body hairs, they do transport pollen and play a role in pollination. Also, many are cleptoparasites of sunflower oligoleges and are important factors in the population ecology of the pollen-collecting bees that visit the flowers of *Helianthus*.

In these lists each bee taxon is followed by the species of *Helianthus* it is known to visit.

OLIGOLEGES OF COMPOSITAE PRIMARILY ASSOCIATED WITH *Helianthus*

- Andrena accepta*: *Helianthus angustifolius*, *H. annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. radula*, *H. rigidus*, *H. salicifolius*, *H. strumosus*, *H. tuberosus*
- Andrena aliciae*: *Helianthus angustifolius*, *H. divaricatus*, *H. giganteus*, *H. microcephalus*, *H. strumosus*, *H. tuberosus*
- Andrena haynesi*: *Helianthus petiolaris*
- Andrena helianthi*: *Helianthus annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. nuttallii*, *H. petiolaris*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
- Andrena peckhami*: *Helianthus strumosus*
- Diadasia enavata*: *Helianthus annuus*, *H. gracilentus*, *H. lenticularis*
- Dufourea marginata*: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. petiolaris*, *H. radula*, *H. rigidus*, *H. tuberosus*
- Exomalopsis pygmaea*: *Helianthus annuus*, *H. lenticularis*
- Hesperapis carinata*: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*, *H. rigidus*
- Heteranthidium cordaticeps*: *Helianthus annuus*
- Heteranthidium occidentale*: *Helianthus lenticularis*
- Heteranthidium zebatum*: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*, *H. pumilus*, *H. radula*, *H. rigidus*
- Megachile parallela*: *Helianthus annuus*, *H. atrorubens*, *H. divaricatus*, *H. gracilentus*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. nuttallii*, *H. petiolaris*, *H. radula*

- Melissodes agilis*: *Helianthus annuus*, *H. atrorubens*, *H. bolanderi*, *H. ciliaris*, *H. divaricatus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. pumilus*, *H. radula*, *H. rigidus*, *H. salicifolius*, *H. strumosus*, *H. tuberosus*
- Melissodes coloradensis*: *Helianthus annuus*, *H. atrorubens*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. petiolaris*, *H. rigidus*, *H. tuberosus*
- Melissodes coreopsis*: *Helianthus annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. salicifolius*, *H. tuberosus*
- Melissodes gelida*: *Helianthus annuus*, *H. petiolaris*
- Melissodes perlusa*: *Helianthus annuus*, *H. petiolaris*
- Melissodes robustior*: *Helianthus annuus*, *H. bolanderi*, *H. gracilentus*, *H. lenticularis*, *H. petiolaris*
- Melissodes trinodis*: *Helianthus annuus*, *H. atrorubens*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. maximiliani*, *H. mollis*, *H. salicifolius*, *H. strumosus*, *H. tuberosus*
- Nomia heteropoda*: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*, *H. radula*
- Nomia micheneri*: *Helianthus petiolaris*
- Nomia triangulifera*: *Helianthus annuus*, *H. lenticularis*, *H. maximiliani*, *H. petiolaris*
- Perdita albipennis*: *Helianthus annuus*, *H. lenticularis*, *H. occidentalis*, *H. petiolaris*, *H. rigidus*
- Perdita bequaerti*: *Helianthus divaricatus*, *H. radula*
- Perdita laticincta*: *Helianthus petiolaris*
- Perdita lingualis*: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*
- Perdita scopata*: *Helianthus annuus*
- Perdita tricineta*: *Helianthus annuus*
- Perdita tridentata*: *Helianthus petiolaris*, *H. rigidus*
- Pseudopanurgus aethiops*: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*
- Pseudopanurgus rugosus*: *Helianthus annuus*, *H. divaricatus*, *H. petiolaris*, *H. mollis*, *H. radula*, *H. tuberosus*
- Pterosarus helianthi*: *Helianthus annuus*, *H. petiolaris*
- Pterosarus innuptus*: *Helianthus annuus*, *H. maximiliani*, *H. nuttallii*, *H. petiolaris*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
- Pterosarus piercei piercei*: *Helianthus annuus*, *H. maximiliani*, *H. petiolaris*, *H. rigidus*, *H. tuberosus*
- Pterosarus simulans*: *Helianthus annuus*, *H. maximiliani*, *H. petiolaris*
- Svastra helianthelli*: *Helianthus annuus*, *H. ciliaris*
- Svastra machaerantherae*: *Helianthus annuus*, *H. petiolaris*
- Svastra obliqua*: *Helianthus annuus*, *H. atrorubens*, *H. bolanderi*, *H. ciliaris*, *H. divaricatus*, *H. gracilentus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. microcephalus*, *H. mollis*, *H. petiolaris*, *H. rigidus*, *H. strumosus*, *H. tuberosus*

OLIGOLEGES OF COMPOSITAE SECONDARILY ASSOCIATED WITH *Helianthus*

- Andrena chromotricha*: *Helianthus annuus*, *H. giganteus*, *H. maximiliani*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
- Andrena duplicata*: *Helianthus divaricatus*, *H. grosseserratus*
- Andrena pallidifovea*: *Helianthus gracilentus*

- Andrena pecosana*: *Helianthus petiolaris*
Andrena simplex: *Helianthus tuberosus*
Anthocopa hemizoniae: *Helianthus gracilentus*
Ashmeadiella buconis: *Helianthus divaricatus*, *H. gracilentus*, *H. petiolaris*
Ashmeadiella californica: *Helianthus annuus*, *H. gracilentus*
Calliopsis crypta: *Helianthus* sp.
Calliopsis pectidis: *Helianthus* sp.
Calliopsis pugionis: *Helianthus gracilentus*
Calliopsis rozeni: *Helianthus annuus*
Colletes compactus: *Helianthus tuberosus*
Colletes rufocinctus: *Helianthus annuus*, *H. petiolaris*
Colletes simulans armatus: *Helianthus petiolaris*
Colletes susanna: *Helianthus petiolaris*
Dianthidium curvatum sayi: *Helianthus annuus*, *H. lenticularis*, *H. maximiliani*, *H. petiolaris*
Hesperapis arenicola: *Helianthus niveus*
Heteranthidium timberlakei: *Helianthus gracilentus*
Megachile alata: *Helianthus gracilentus*
Megachile dakotensis: *Helianthus* sp.
Megachile helianthi: *Helianthus lenticularis*
Megachile inimica: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. petiolaris*, *H. rigidus*, *H. tuberosus*
Megachile manifesta: *Helianthus annuus*, *H. petiolaris*
Megachile pugnata pugnata: *Helianthus annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. strumosus*, *H. tuberosus*
Megachile sabinensis: *Helianthus* sp.
Megachile xerophila: *Helianthus niveus*
Melissodes appressa: *Helianthus annuus*
Melissodes bidentis: *Helianthus annuus*, *H. maximiliani*, *H. tuberosus*
Melissodes bimatrix: *Helianthus* sp.
Melissodes brevipygga: *Helianthus annuus*
Melissodes composita: *Helianthus annuus*
Melissodes confusa: *Helianthus annuus*
Melissodes dentiventris: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. radula*
Melissodes glenwoodensis: *Helianthus petiolaris*
Melissodes grindeliae: *Helianthus* sp.
Melissodes humilior: *Helianthus annuus*
Melissodes illata: *Helianthus strumosus*
Melissodes limbis: *Helianthus annuus*
Melissodes lupina: *Helianthus annuus*, *H. gracilentus*, *H. nuttallii*
Melissodes lustra: *Helianthus* sp.
Melissodes lutulenta: *Helianthus* sp.
Melissodes menuachus: *Helianthus annuus*, *H. grosseserratus*, *H. petiolaris*
Melissodes microsticta: *Helianthus* sp.
Melissodes montana: *Helianthus annuus*, *H. petiolaris*
Melissodes nivea: *Helianthus annuus*, *H. atrorubens*, *H. divaricatus*, *H. grosseserratus*
Melissodes pallidesignata: *Helianthus* sp.
Melissodes paulula: *Helianthus annuus*
Melissodes rivalis: *Helianthus annuus*
Melissodes rustica: *Helianthus atrorubens*, *H. divaricatus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. radula*, *H. strumosus*, *H. tuberosus*
Melissodes snowii: *Helianthus petiolaris*, *H. rigidus*
Melissodes stearnsi: *Helianthus annuus*
Melissodes subagilis: *Helianthus annuus*, *H. maximiliani*, *H. petiolaris*
Melissodes subillata: *Helianthus maximiliani*, *H. petiolaris*
Melissodes tinctoria: *Helianthus maximiliani*
Melissodes vernoniae: *Helianthus divaricatus*, *H. tuberosus*
Melissodes wheeleri: *Helianthus annuus*, *H. debilis*, *H. petiolaris*
Nomia apacha: *Helianthus* sp.
Nomia bolliana: *Helianthus* sp.
Osmia californica: *Helianthus nuttallii*
Osmia coloradensis: *Helianthus gracilentus*
Osmia montana: *Helianthus annuus*, *H. gracilentus*
Osmia texana: *Helianthus* sp.
Paranthidium jugatorium: *Helianthus divaricatus*, *H. lenticularis*, *H. strumosus*
Perdita affinis: *Helianthus petiolaris*
Perdita alexi: *Helianthus petiolaris*
Perdita aridella: *Helianthus petiolaris*
Perdita bruneri: *Helianthus petiolaris*
Perdita dolichocephala: *Helianthus petiolaris*, *H. rigidus*
Perdita fallax: *Helianthus petiolaris*
Perdita ignota crawfordi: *Helianthus annuus*
Perdita nebrascensis: *Helianthus* sp.
Perdita nigroviridis: *Helianthus annuus*
Perdita pratti: *Helianthus debilis*, *H. petiolaris*
Perdita prionopsidis: *Helianthus petiolaris*
Perdita swenki: *Helianthus maximiliani*
Perdita verbesinae: *Helianthus annuus*, *H. petiolaris*
Perdita xanthisma: *Helianthus annuus*, *H. petiolaris*
Pterosarus albitarsis: *Helianthus divaricatus*, *H. mollis*
Pterosarus labrosiformis labrosiformis: *Helianthus divaricatus*, *H. strumosus*, *H. tuberosus*
Pterosarus labrosus: *Helianthus divaricatus*, *H. tuberosus*
Pterosarus occiduus: *Helianthus* sp.
Pterosarus perlaevis: *Helianthus annuus*
Pterosarus renimaculatus: *Helianthus maximiliani*, *H. petiolaris*
Pterosarus rudbeckiae: *Helianthus divaricatus*
Pterosarus solidaginis: *Helianthus grosseserratus*, *H. tuberosus*
Pterosarus stigmalis: *Helianthus lenticularis*
Svastra aegis: *Helianthus annuus*, *H. radula*
Svastra petulca: *Helianthus annuus*
Svastra texana: *Helianthus annuus*, *H. radula*
Syntrichalonia exquisita: *Helianthus petiolaris*

REGULAR POLYLEGES ASSOCIATED WITH *Helianthus*

- Agapostemon texanus*: *Helianthus annuus*, *H. gracilentus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. petiolaris*
Bombus fraternus: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. petiolaris*, *H. rigidus*

- Bombus griseocollis*: *Helianthus annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Bombus morrisoni: *Helianthus annuus*
Bombus nevadensis: *Helianthus annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. rigidus*, *H. tuberosus*
Bombus pennsylvanicus pennsylvanicus: *Helianthus annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Bombus pennsylvanicus sonorus: *Helianthus annuus*, *H. petiolaris*
Halictus ligatus: *Helianthus annuus*, *H. debilis*, *H. divaricatus*, *H. grosseserratus*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. radula*, *H. rigidus*, *H. tuberosus*
Heriades variolosa variolosa: *Helianthus* sp.
Hoplitis producta: *Helianthus petiolaris*
Megachile brevis: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Megachile fidelis: *Helianthus gracilentus*, *H. petiolaris*
Megachile fortis: *Helianthus petiolaris*, *H. rigidus*
Megachile montivaga: *Helianthus annuus*, *H. gracilentus*
Megachile perihirta: *Helianthus annuus*, *H. petiolaris*
Megachile polycaris: *Helianthus annuus*, *H. petiolaris*
Melissodes bimaculata bimaculata: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. tuberosus*
Melissodes boltoniae: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. tuberosus*
Melissodes communis communis: *Helianthus annuus*, *H. debilis*, *H. lenticularis*
Melissodes comptoides: *Helianthus annuus*, *H. petiolaris*
Melissodes sonorensis: *Helianthus petiolaris*
Melissodes tessellata: *Helianthus annuus*

CASUAL POLYLEGES ASSOCIATED WITH *Helianthus*

- Agapostemon angelicus*: *Helianthus annuus*, *H. gracilentus*
Agapostemon cockerelli: *Helianthus annuus*
Agapostemon femoratus: *Helianthus gracilentus*
Agapostemon melliventris: *Helianthus annuus*, *H. niveus*
Agapostemon sericeus: *Helianthus grosseserratus*, *H. strumosus*
Agapostemon splendens: *Helianthus debilis*
Agapostemon tyleri: *Helianthus annuus*
Agapostemon virescens: *Helianthus* sp.
Andrena lawrencei: *Helianthus nuttallii*
Andrena microchlora: *Helianthus* sp.
Andrena prunorum: *Helianthus* sp.
Andrena recta: *Helianthus annuus*
Anthidiellum notatum notatum: *Helianthus* sp.
Anthidiellum perplexum: *Helianthus debilis*
Anthidium pavoselae: *Helianthus mollis*, *H. petiolaris*
Anthophora curta: *Helianthus annuus*, *H. gracilentus*, *H. petiolaris*
Anthophora maculifrons: *Helianthus annuus*
Anthophora montana: *Helianthus annuus*
Anthophora peritomae: *Helianthus annuus*
Apis mellifera: *Helianthus annuus*, *H. giganteus*, *H. strumosus*
Ashmeadiella foveata: *Helianthus gracilentus*
Augochlora pura: *Helianthus debilis*
Augochlorella aurata: *Helianthus* sp.
Augochlorella bracteata: *Helianthus* sp.
Augochlorella gratiosa: *Helianthus* sp.
Augochlorella persimilis: *Helianthus mollis*
Augochlorella striata: *Helianthus giganteus*, *H. lenticularis*, *H. maximiliani*, *H. strumosus*, *H. tuberosus*
Augochlorella metallica metallica: *Helianthus annuus*, *H. debilis*, *H. grosseserratus*, *H. mollis*, *H. strumosus*
Augochloropsis sumptuosa: *Helianthus* sp.
Bombus affinis: *Helianthus giganteus*
Bombus appositus: *Helianthus* sp.
Bombus bimaculatus: *Helianthus annuus*
Bombus borealis: *Helianthus* sp.
Bombus californicus: *Helianthus* sp.
Bombus centralis: *Helianthus strumosus*
Bombus crotchii: *Helianthus* sp.
Bombus fervidus fervidus: *Helianthus annuus*
Bombus huntii: *Helianthus* sp.
Bombus impatiens: *Helianthus annuus*, *H. grosseserratus*
Bombus rufocinctus: *Helianthus* sp.
Bombus ternarius: *Helianthus strumosus*
Bombus terricola: *Helianthus strumosus*
Bombus vagans vagans: *Helianthus annuus*, *H. giganteus*, *H. grosseserratus*, *H. strumosus*, *H. tuberosus*
Callanthidium illustre: *Helianthus* sp.
Ceratina acantha: *Helianthus gracilentus*
Ceratina apacheorum: *Helianthus gracilentus*
Ceratina calcarata: *Helianthus* sp.
Ceratina dupla: *Helianthus annuus*, *H. divaricatus*, *H. maximiliani*, *H. strumosus*
Ceratina micheneri: *Helianthus* sp.
Ceratina nanula: *Helianthus petiolaris*
Ceratina neomexicana: *Helianthus petiolaris*
Ceratina pacifica: *Helianthus annuus*, *H. petiolaris*
Ceratina punctigena: *Helianthus gracilentus*, *H. occidentalis*
Ceratina shimmersi: *Helianthus annuus*
Ceratina strenua: *Helianthus* sp.
Chalicodoma angelarum: *Helianthus annuus*, *H. gracilentus*
Chalicodoma campanulae campanulae: *Helianthus* sp.
Chelostomopsis rubifloris: *Helianthus* sp.
Colletes fulgidus: *Helianthus annuus*
Dialictus imitatus: *Helianthus annuus*
Dialictus incompletus: *Helianthus annuus*
Dialictus marinus: *Helianthus debilis*
Dialictus nevadensis: *Helianthus lenticularis*
Dialictus pilosus pilosus: *Helianthus annuus*, *H. divaricatus*, *H. mollis*, *H. rigidus*, *H. tuberosus*
Dialictus pruinosiformis: *Helianthus annuus*, *H. lenticularis*, *H. petiolaris*
Dialictus punctatovenstris: *Helianthus* sp.
Dialictus tegulariformis: *Helianthus lenticularis*
Dialictus veganus: *Helianthus* sp.

Dialictus versatus: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. rigidus*
Dialictus zephyrus: *Helianthus tuberosus*
Dianthidium dubium dilectum: *Helianthus gracilentus*, *H. petiolaris*
Dianthidium ulkei: *Helianthus petiolaris*
Euylaeus kincaidii: *Helianthus* sp.
Euylaeus pectoralis: *Helianthus divaricatus*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Euylaeus pectoraloides: *Helianthus annuus*
Exomalopsis morgani: *Helianthus* sp.
Exomalopsis solani: *Helianthus annuus*
Exomalopsis solidaginis: *Helianthus annuus*
Halictus confusus: *Helianthus annuus*, *H. divaricatus*, *H. strumosus*
Halictus farinosus: *Helianthus annuus*, *H. gracilentus*
Halictus rubicundus: *Helianthus annuus*, *H. maximiliani*, *H. strumosus*
Halictus tripartitus: *Helianthus annuus*
Heriades carinata: *Helianthus strumosus*
Heriades occidentalis: *Helianthus gracilentus*
Hoplitis cylindrica: *Helianthus strumosus*
Hoplitis pilosifrons: *Helianthus petiolaris*
Hoplitis sambuci: *Helianthus* sp.
Hoplitis simplex: *Helianthus strumosus*
Hoplitis truncata truncata: *Helianthus divaricatus*
Lasioglossum coriaceum: *Helianthus strumosus*, *H. tuberosus*
Lasioglossum sisymbrii: *Helianthus annuus*, *H. niveus*
Lasioglossum titusi: *Helianthus* sp.
Megachile agustini: *Helianthus annuus*, *H. petiolaris*
Megachile albitarsis: *Helianthus divaricatus*, *H. radula*, *H. tuberosus*
Megachile casadae: *Helianthus* sp.
Megachile centuncularis: *Helianthus annuus*, *H. strumosus*
Megachile coquillettii: *Helianthus gracilentus*
Megachile dentitarsus: *Helianthus petiolaris*
Megachile frugalis: *Helianthus gracilentus*, *H. petiolaris*
Megachile gemula gemula: *Helianthus giganteus*
Megachile inermis: *Helianthus giganteus*
Megachile latimanus: *Helianthus annuus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. maximiliani*, *H. mollis*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Megachile lippiae: *Helianthus* sp.
Megachile melanophaea: *Helianthus giganteus*
Megachile mendica: *Helianthus annuus*, *H. divaricatus*, *H. radula*, *H. strumosus*
Megachile mucronosa: *Helianthus annuus*
Megachile petulans: *Helianthus atrorubens*, *H. divaricatus*, *H. mollis*, *H. strumosus*
Megachile pruina pruina: *Helianthus* sp.
Megachile relativa: *Helianthus giganteus*, *H. grosseserratus*
Megachile texana: *Helianthus annuus*, *H. grosseserratus*
Megachile townsendiana: *Helianthus annuus*, *H. debilis*
Megachile xylocopoides: *Helianthus ciliaris*
Megachile zapoteca: *Helianthus* sp.
Melissodes desponsa: *Helianthus annuus*, *H. grosseserratus*, *H. strumosus*
Melissodes denticulata: *Helianthus debilis*

Melissodes opuntiella: *Helianthus annuus*
Melissodes paroselae: *Helianthus annuus*
Melissodes tepida: *Helianthus annuus*, *H. bolanderi*, *H. petiolaris*
Melissodes thelypodii thelypodii: *Helianthus annuus*
Melissodes tristis: *Helianthus annuus*, *H. ciliaris*, *H. petiolaris*
Nomia nortoni nortoni: *Helianthus maximiliani*
Osmia clarescens: *Helianthus gracilentus*
Osmia grinnelli: *Helianthus gracilentus*
Osmia marginata: *Helianthus annuus*, *H. gracilentus*, *H. niveus*
Osmia subfasciata subfasciata: *Helianthus* sp.
Perdita gerhardi dallasiana: *Helianthus annuus*
Protandrena bancrofti: *Helianthus* sp.
Svastra atripes atripes: *Helianthus annuus*
Svastra cressonii: *Helianthus annuus*
Synhalonia actuosa: *Helianthus nuttallii*
Synhalonia edwardsii: *Helianthus annuus*

NECTAR VISITORS NOT KNOWN TO TAKE POLLEN FROM *Helianthus*

Anthidium maculosum: *Helianthus annuus*
Anthidium porterae: *Helianthus annuus*, *H. petiolaris*
Anthophora smithii: *Helianthus annuus*
Anthophora urbana urbana: *Helianthus annuus*, *H. gracilentus*
Anthophora walshii: *Helianthus grosseserratus*, *H. petiolaris*
Ashmeadiella titusi: *Helianthus gracilentus*
Augochlorella pomoniella: *Helianthus annuus*
Calliopsis andreniformis: *Helianthus strumosus*
Centris atripes: *Helianthus annuus*
Centris caesalpiniae: *Helianthus annuus*
Ceratina dallatorreana: *Helianthus annuus*
Ceratina tejonensis: *Helianthus gracilentus*
Chalicodoma chilopsidis: *Helianthus* sp.
Chalicodoma occidentalis: *Helianthus annuus*
Chalicodoma odontostoma: *Helianthus* sp.
Chalicodoma spinotulata: *Helianthus* sp.
Chalicodoma subexilis: *Helianthus* sp.
Colletes americanus: *Helianthus divaricatus*
Colletes louisae: *Helianthus annuus*
Colletes perileucus: *Helianthus annuus*
Colletes wootoni: *Helianthus annuus*
Diadasia afflicta afflicta: *Helianthus* sp.
Diadasia australis: *Helianthus gracilentus*
Diadasia bituberculata: *Helianthus annuus*
Diadasia diminuta: *Helianthus annuus*, *H. gracilentus*, *H. petiolaris*
Diadasia ochracea: *Helianthus annuus*
Diadasia rinconis rinconis: *Helianthus annuus*
Dialictus albipennis: *Helianthus strumosus*
Dialictus clematisellus: *Helianthus annuus*
Dialictus illinoensis: *Helianthus divaricatus*
Dialictus impavidus: *Helianthus gracilentus*, *H. sp.*
Dialictus microlepidus: *Helianthus annuus*
Dialictus oleosus: *Helianthus annuus*
Euylaeus aberrans: *Helianthus petiolaris*

Evylaeus amicus: *Helianthus annuus*
Evylaeus argemonis: *Helianthus annuus*
Evylaeus pectinatus: *Helianthus tuberosus*
Hoplitis biscutellae: *Helianthus niveus*
Lasioglossum mellipes: *Helianthus gracilentus*
Lithurge gibbosus: *Helianthus* sp.
Martinapis occidentalis: *Helianthus niveus*
Megachile coloradensis: *Helianthus annuus*
Megachile concinna: *Helianthus annuus*
Megachile gentilis: *Helianthus annuus*
Megachile nevadensis: *Helianthus gracilentus*
Megachile sidalceae: *Helianthus annuus*, *H. ciliaris*
Melissodes fimbriata: *Helianthus petiolaris*
Melissodes plumosa: *Helianthus petiolaris*
Melissodes velutina: *Helianthus gracilentus*
Melissodes verbesinarum: *Helianthus annuus*
Metapsaenythia abdominalis abdominalis: *Helianthus annuus*
Nomadopsis helianthi: *Helianthus* sp.
Nomia angustitibialis: *Helianthus annuus*
Nomia fedorensis: *Helianthus* sp.
Nomia melanderi: *Helianthus* sp.
Nomia mesillensis: *Helianthus annuus*
Nomia nevadensis angelesia: *Helianthus annuus*, *H. gracilentus*
Nomia nevadensis arizonensis: *Helianthus annuus*
Peponapis pruinosa: *Helianthus annuus*
Perdita zebra zebra: *Helianthus petiolaris*
Protandrena mexicanorum: *Helianthus annuus*
Protoxaea gloriosa: *Helianthus annuus*
Pterosarus expallidus: *Helianthus* sp.
Pterosarus leucopterus: *Helianthus petiolaris*
Ptilothrix sp. near *sumichrasti*: *Helianthus annuus*
Svastra grandissima: *Helianthus annuus*
Svastra sabinensis: *Helianthus annuus*
Svastra sila: *Helianthus annuus*
Xenoglossodes bishoppi: *Helianthus* sp.
Xenoglossodes eriocarpi: *Helianthus annuus*
Xenoglossodes helianthorum: *Helianthus* sp.
Xylocopa californica: *Helianthus annuus*

PARASITIC BEES KNOWN TO VISIT THE FLOWERS OF *Helianthus*

Coelioxys alternata: *Helianthus divaricatus*
Coelioxys banksi: *Helianthus* sp.
Coelioxys edita: *Helianthus annuus*
Coelioxys funeraria: *Helianthus strumosus*
Coelioxys germana: *Helianthus divaricatus*
Coelioxys menthae: *Helianthus annuus*
Coelioxys modesta: *Helianthus strumosus*
Coelioxys moesta: *Helianthus giganteus*
Coelioxys novomexicana: *Helianthus* sp.
Coelioxys octodentata: *Helianthus divaricatus*, *H. mollis*, *H. strumosus*
Coelioxys rufitarsus: *Helianthus grosseserratus*, *H. strumosus*
Coelioxys sayi: *Helianthus divaricatus*, *H. strumosus*
Coelioxys sodalis: *Helianthus strumosus*

Coelioxys texana: *Helianthus strumosus*
Dioxys aurifuscus: *Helianthus* sp.
Dioxys pomonae pomonae: *Helianthus* sp.
Epeolus autumnalis: *Helianthus divaricatus*, *H. tuberosus*
Epeolus bifasciatus: *Helianthus divaricatus*
Epeolus compactus: *Helianthus divaricatus*
Epeolus pusillus: *Helianthus divaricatus*
Holcopasites heliopsis: *Helianthus* sp.
Neolarra helianthi: *Helianthus petiolaris*
Neolarra verbesinae: *Helianthus petiolaris*
Nomada garciana: *Helianthus* sp.
Nomada graenicheri: *Helianthus giganteus*, *H. strumosus*
Nomada gutierreziae: *Helianthus* sp.
Nomada melanoptera: *Helianthus petiolaris*
Nomada texana: *Helianthus* sp.
Nomada vierecki: *Helianthus petiolaris*
Nomada vineta vineta: *Helianthus grosseserratus*, *H. strumosus*, *H. tuberosus*
Paranomada velutina: *Helianthus* sp.
Psithyrus ashtoni: *Helianthus* sp.
Psithyrus citrinus: *Helianthus strumosus*
Psithyrus insularis: *Helianthus* sp.
Psithyrus variabilis: *Helianthus annuus*, *H. grosseserratus*, *H. petiolaris*, *H. rigidus*
Sphecodes dichrous: *Helianthus* sp.
Triepeolus concavus: *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. rigidus*, *H. strumosus*, *H. tuberosus*
Triepeolus cressonii cressonii: *Helianthus divaricatus*, *H. grosseserratus*, *H. mollis*, *H. strumosus*
Triepeolus cyclurus: *Helianthus petiolaris*
Triepeolus dacotensis: *Helianthus petiolaris*
Triepeolus donatus: *Helianthus divaricatus*, *H. grosseserratus*, *H. strumosus*
Triepeolus helianthi: *Helianthus divaricatus*, *H. grosseserratus*
Triepeolus lestes: *Helianthus annuus*
Triepeolus lineatulus: *Helianthus annuus*, *H. bolanderi*
Triepeolus lunatus: *Helianthus divaricatus*, *H. tuberosus*
Triepeolus nevadensis: *Helianthus divaricatus*
Triepeolus norae: *Helianthus annuus*
Triepeolus pectoralis: *Helianthus strumosus*
Triepeolus rectangularis: *Helianthus* sp.
Triepeolus remigatus: *Helianthus divaricatus*, *H. lenticularis*
Triepeolus simplex: *Helianthus divaricatus*
Triepeolus subnitens: *Helianthus annuus*
Triepeolus texanus: *Helianthus ciliaris*
Triepeolus trichopygus: *Helianthus annuus*
Xeromelecta californica: *Helianthus annuus*, *H. lenticularis*
Xeromelecta interrupta: *Helianthus annuus*

SPECIES OF *Helianthus* WITH KNOWN BEE VISITORS

To facilitate future pollination studies of particular species of *Helianthus* we have listed below in alphabetical order the species of *Helianthus* with

known bee visitors. The taxa of bees are then listed alphabetically for each of these species. It will be noticed that some species of *Helianthus* have fewer taxa of bees associated with them than others. Doubtless some of this is simply due to the lack of detailed field studies, but at least in some cases it may be that some species of *Helianthus* are less attractive than others. For example, Graenicher (1909:68) has commented on his studies of *H. giganteus* that these flowers do not seem to be as attractive to insects (including bees) as those of *H. strumosus*. Also, it is to be expected that those species of *Helianthus* with widespread distribution, e.g., *H. annuus* and *H. petiolaris*, will have a greater number of bee visitors than those species with more restricted distributions. Our knowledge of the oligoleges primarily associated with *Helianthus* is summarized in Table N.

Helianthus angustifolius: *Andrena accepta*, *A. aliciae*

Helianthus annuus: *Agapostemon angelicus*, *A. cockerelli*, *A. melliventris*, *A. texanus*, *A. tyleri*, *Andrena accepta*, *A. chromotricha*, *A. helianthi*, *A. recta*, *Anthidium maculosum*, *A. porterae*, *Anthophora curta*, *A. maculifrons*, *A. montana*, *A. peritomae*, *A. smithii*, *A. urbana urbana*, *Apis mellifera*, *Ashmeadiella californica*, *Augochlorella pomoniella*, *Augochloropsis metallica metallica*, *Bombus bimaculatus*, *B. fervidus fervidus*, *B. fraternus*, *B. griseocollis*, *B. impatiens*, *B. morrisoni*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *B. p. sonorus*, *B. vagans vagans*, *Calliopsis rozeni*, *Centris atripes*, *C. caesalpiniae*, *Ceratina dallatorreana*, *C. dupla*, *C. pacifica*, *C. shinersi*, *Chalicodoma angelarum*, *C. occidentalis*, *Coelioxys edita*, *C. menthae*, *Colletes fulgidus*, *C. louisae*, *C. perileucus*, *C. rufocinctus*, *C. wootoni*, *Diadasia bituberculata*, *D. diminuta*, *D. enavata*, *D. ochracea*, *D. rinconis rinconis*, *Dialictus clematisellus*, *D. imitatus*, *D. incompletus*, *D. microlepidus*, *D. oleosus*, *D. pilosus pilosus*, *D. pruiniformis*, *D. versatus*, *Dianthidium curvatum sayi*, *Dufourea marginata*, *Evylaeus amicus*, *E. argemonis*, *E. pectoraloides*, *Exomalopsis pygmaea*, *E. solani*, *E. solidaginis*, *Halictus confusus*, *H. farinosus*, *H. ligatus*, *H. rubicundus*, *H. tripartitus*, *Hesperapis carinata*, *Heteranthidium cordaticeps*, *H. zeburatum*, *Lasioglossum sisymbrii*, *Megachile agustini*, *M. brevis*, *M. centuncularis*, *M. coloradensis*, *M. concinna*, *M. gentilis*, *M. inimica*, *M. latimanus*, *M. manifesta*, *M. mendica*, *M. montivaga*, *M. mucronata*, *M. nevadensis*, *M. parallela*, *M. perihirta*, *M. pollicaris*, *M. pugnata pugnata*, *M. sidalceae*, *M. texana*, *M. townsendiana*, *Melissodes agilis*, *M. appressa*, *M. bidens*, *M. bimaculata*, *M. boltoniae*, *M. brevipygga*, *M. coloradensis*, *M. communis communis*, *M. composita*, *M. comptoides*, *M. confusa*, *M. coreopsis*, *M. dentiventris*, *M. desponsa*, *M. gelida*, *M. humilior*, *M. limbus*, *M. lupina*, *M. menuachus*, *M. montana*, *M. nivea*, *M. opuntiella*, *M. paroselae*, *M. paulula*, *M. perlusa*, *M. rivalis*, *M. robustior*, *M. stearnsi*, *M.*

subagilis, *M. submenuacha*, *M. tepida*, *M. tessellata*, *M. thelypodii thelypodii*, *M. trinodis*, *M. tristis*, *M. verbesinarum*, *M. wheeleri*, *Metapsaenythia abdominalis abdominalis*, *Nomia angustitibialis*, *N. heteropoda*, *N. mesillensis*, *N. nevadensis angelesia*, *N. n. arizonensis*, *N. triangulifera*, *Osmia marginata*, *O. montana*, *Paranomada velutina*, *Peponapis pruinosa*, *Perdita albipennis*, *P. ignota crawfordi*, *P. gerhardi dallasiana*, *P. lingualis*, *P. nigroviridis*, *P. scopata*, *P. tricineta*, *P. verbesinae*, *P. xanthisma*, *Protandrena mexicanorum*, *Protophaga gloriosa*, *Pseudopanurgus aethiops*, *P. rugosus*, *Psithyrus variabilis*, *Pterosarus helianthi*, *P. innuptus*, *P. perlaevis*, *P. piercei piercei*, *P. simulans*, *Ptilothrix* sp. near *sumichrasti*, *Svastra aegis*, *S. atripes atripes*, *S. cressonii*, *S. grandissima*, *S. helianthelli*, *S. machaerantherae*, *S. obliqua*, *S. petulca*, *S. sabinensis*, *S. sila*, *S. texana*, *Synhalonia edwardsii*, *Triepeolus concavus*, *T. lestes*, *T. lineatulus*, *T. norae*, *T. subnitens*, *T. trichopygus*, *Xenoglossodes eriocarpi*, *Xeromelecta californica*, *X. interrupta*, *Xylocopa californica*

Helianthus atrorubens: *Megachile parallela*, *M. petulans*, *Melissodes agilis*, *M. coloradensis*, *M. nivea*, *M. rustica*, *M. trinodis*, *Svastra obliqua*

Helianthus bolanderi: *Melissodes agilis*, *M. robustior*, *M. tepida*, *Triepeolus lineatulus*, *Svastra obliqua*

Helianthus ciliaris: *Megachile sidalceae*, *M. xylocopoides*, *Melissodes agilis*, *M. tristis*, *Svastra helianthelli*, *S. obliqua*, *Triepeolus texanus*

Helianthus debilis: *Agapostemon splendens*, *Anthidiellum perplexum*, *Augochlora pura*, *Augochloropsis metallica metallica*, *Dialictus marinus*, *Halictus ligatus*, *Megachile townsendiana*, *Melissodes communis communis*, *M. denticulata*, *M. wheeleri*, *Perdita pratti*

Helianthus divaricatus: *Andrena accepta*, *A. aliciae*, *A. duplicata*, *A. helianthi*, *Ashmeadiella buconis*, *Bombus fraternus*, *B. griseocollis*, *B. pennsylvanicus pennsylvanicus*, *Ceratina dupla*, *Coelioxys alternata*, *C. germana*, *C. octodentata*, *C. sayi*, *Colletes americanus*, *Dialictus illinoensis*, *D. pilosus pilosus*, *D. versatus*, *Dufourea marginata*, *Epeolus autumnalis*, *E. bifasciatus*, *E. compactus*, *E. pusillus*, *Evylaeus pectoralis*, *Halictus confusus*, *H. ligatus*, *Hoplitis truncata truncata*, *Megachile albitarsis*, *M. brevis*, *M. inimica*, *M. latimanus*, *M. mendica*, *M. parallela*, *M. petulans*, *M. pugnata pugnata*, *Melissodes agilis*, *M. bimaculata bimaculata*, *M. boltoniae*, *M. coloradensis*, *M. dentiventris*, *M. nivea*, *M. rustica*, *M. trinodis*, *M. vernoniae*, *Paranthidium jugatorium*, *Perdita bequaerti*, *Pseudopanurgus rugosus*, *Pterosarus albitarsis*, *P. labrosiformis labrosiformis*, *P. labrosus*, *P. rudbeckiae*, *Svastra obliqua*, *Triepeolus concavus*, *T. cressonii cressonii*, *T. donatus*, *T. helianthi*, *T. lunatus*, *T. nevadensis*, *T. remigatus*, *T. simplex*

Helianthus giganteus: *Andrena accepta*, *A. aliciae*, *A. chromotricha*, *A. helianthi*, *Apis mellifera*, *Augochlorella striata*, *Bombus affinis*, *B. griseocollis*, *B. pennsylvanicus pennsylvanicus*, *B. vagans vagans*, *Coelioxys moesta*, *Megachile gemula gemula*, *M. inermis*, *M. latimanus*, *M. melanophaea*, *M. pugnata pugnata*, *M. relativa*, *Melissodes trinodis*, *Nomada graenicheri*

Helianthus gracilentus: *Agapostemon angelicus*, *A. femoratus*, *A. texanus*, *Andrena pallidifovea*, *Anthocopa hemizoniae*, *Anthophora curta*, *A. urbana urbana*, *Ashmeadiella buconis*, *A. californica*, *A. foveata*, *A. titusi*, *Calliopsis pugionis*, *Ceratina acantha*, *C. apa-*

- cheorum*, *C. punctigena*, *C. tejonensis*, *Chalicodoma angelarum*, *Diadasia australis*, *D. enavata*, *Dialictus impavidus*, *Dianthidium dubium dilectum*, *Halictus farinosus*, *Heriades occidentalis*, *Heteranthidium timberlakei*, *Lasioglossum mellipes*, *Megachile alata*, *M. coquilletti*, *M. fidelis*, *M. frugalis*, *M. montivaga*, *M. nevadensis*, *M. parallela*, *Melissodes lupina*, *M. robustior*, *M. velutina*, *Nomia nevadensis angelesia*, *Osmia clarescens*, *O. coloradensis*, *O. grinnelli*, *O. marginata*, *O. montana*, *Svastra obliqua*, *Xeromelecta californica*
- Helianthus grosseserratus*: *Agapostemon sericeus*, *A. texanus*, *Andrena accepta*, *A. duplicata*, *A. helianthi*, *Anthophora walshii*, *Augochloropsis metallica metallica*, *Bombus fraternus*, *B. griseocollis*, *B. impatiens*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *B. vagans vagans*, *Coelioxys rufitarsus*, *Dialictus versatus*, *Dufourea marginata*, *Halictus ligatus*, *Megachile brevis*, *M. inimica*, *M. latimanus*, *M. pugnata pugnata*, *M. relativa*, *M. texana*, *Melissodes agilis*, *M. bimaculata bimaculata*, *M. boltoniae*, *M. coloradensis*, *M. coreopsis*, *M. dentiventris*, *M. desponsa*, *M. menuachus*, *M. nivea*, *M. rustica*, *M. trinodis*, *Nomada vincta vincta*, *Psithyrus variabilis*, *Pterosarus solidaginis*, *Svastra obliqua*, *Triepeolus concavus*, *T. cressonii cressonii*, *T. donatus*, *T. helianthi*
- Helianthus lenticularis*: *Agapostemon texanus*, *Andrena accepta*, *A. helianthi*, *Augochlorella striata*, *Bombus pennsylvanicus pennsylvanicus*, *Diadasia enavata*, *Dialictus nevadensis*, *D. pruinosiformis*, *D. regulariformis*, *Dianthidium curvatum sayi*, *Exomalopsis pygmaea*, *Halictus ligatus*, *Hesperapis carinata*, *Heteranthidium occidentale*, *H. zebratum*, *Megachile helianthi*, *M. parallela*, *Nomia heteropoda*, *Melissodes agilis*, *M. communis communis*, *M. robustior*, *Nomia triangulifera*, *Paranthidium jugatorium*, *Perdita albipennis*, *P. lingualis*, *Pseudopanurgus aethiops*, *Pterosarus stigmatalis*, *Svastra obliqua*, *Triepeolus remigatus*, *Xeromelecta californica*
- Helianthus maximiliani*: *Agapostemon texanus*, *Andrena accepta*, *A. chromotricha*, *A. helianthi*, *Augochlorella striata*, *Bombus griseocollis*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *Ceratina dupla*, *Dianthidium curvatum sayi*, *Halictus ligatus*, *H. rubicundus*, *Megachile latimanus*, *M. parallela*, *Melissodes agilis*, *M. bidentis*, *M. coreopsis*, *M. rustica*, *M. subagilis*, *M. subillata*, *M. tincta*, *M. trinodis*, *Nomia nortoni nortoni*, *N. triangulifera*, *Perdita swenki*, *Pterosarus innuptus*, *P. piercei piercei*, *P. renimaculatus*, *P. simulans*, *Svastra obliqua*
- Helianthus microcephalus*: *Andrena aliciae*, *Svastra obliqua*
- Helianthus mollis*: *Andrena accepta*, *Anthidium paroselae*, *Augochlorella persimilis*, *Augochloropsis metallica metallica*, *Bombus pennsylvanicus pennsylvanicus*, *Coelioxys octodentata*, *Dialictus pilosus pilosus*, *D. versatus*, *Halictus ligatus*, *Megachile brevis*, *M. latimanus*, *M. parallela*, *M. petulans*, *Melissodes agilis*, *M. coloradensis*, *M. trinodis*, *Pseudopanurgus rugosus*, *Pterosarus albitarsis*, *Svastra obliqua*, *Triepeolus concavus*, *T. cressonii cressonii*
- Helianthus niveus*: *Agapostemon melliventris*, *Hesperapis arenicola*, *Hoplitis biscutellae*, *Lasioglossum sisymbrii*, *Martinapis occidentalis*, *Megachile xerophila*, *Osmia marginata*
- Helianthus nuttallii*: *Andrena helianthi*, *A. lawrencei*, *Megachile parallela*, *Melissodes lupina*, *Osmia californica*, *Pterosarus innuptus*, *Synhalonia actuosa*
- Helianthus occidentalis*: *Ceratina punctigena*, *Perdita albipennis*
- Helianthus petiolaris*: *Agapostemon texanus*, *Andrena accepta*, *A. haynesi*, *A. helianthi*, *A. pecosana*, *Anthidium paroselae*, *A. porterae*, *Anthophora curta*, *A. walshii*, *Ashmeadiella buconis*, *Bombus fraternus*, *B. griseocollis*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *B. p. sonorus*, *Ceratina nanula*, *C. neomexicana*, *C. pacifica*, *Colletes rufocinctus*, *C. simulans armatus*, *C. susannae*, *Diadasia diminuta*, *Dialictus pruinosiformis*, *Dianthidium curvatum sayi*, *D. dubium dilectum*, *D. ulkei*, *Dufourea marginata*, *Evyllaenus aberrans*, *Halictus ligatus*, *Hesperapis carinata*, *Heteranthidium zebratum*, *Hoplitis pilosifrons*, *H. producta*, *Megachile agustini*, *M. dentitarsus*, *M. fidelis*, *M. fortis*, *M. frugalis*, *M. inimica*, *M. manifesta*, *M. parallela*, *M. perihirta*, *M. polycaris*, *Melissodes agilis*, *M. coloradensis*, *M. comptoides*, *M. coreopsis*, *M. fimbriata*, *M. gelida*, *M. glenwoodensis*, *M. menuachus*, *M. montana*, *M. perlusa*, *M. plumosa*, *M. robustior*, *M. rustica*, *M. snowii*, *M. sonorensis*, *M. subagilis*, *M. subillata*, *M. submenuacha*, *M. tepida*, *M. tristis*, *M. wheeleri*, *Neolarra helianthi*, *N. verbesinae*, *Nomada melanoptera*, *N. vierecki*, *Nomia heteropoda*, *N. micheneri*, *N. triangulifera*, *Perdita affinis*, *P. albipennis*, *P. alexi*, *P. aridella*, *P. bruneri*, *P. dolichocephala*, *P. fallax*, *P. laticincta*, *P. lingualis*, *P. pratti*, *P. prionopsidis*, *P. tridentata*, *P. verbesinae*, *P. xanthisma*, *P. zebrata zebrata*, *Pseudopanurgus aethiops*, *P. rugosus*, *Psithyrus variabilis*, *Pterosarus helianthi*, *P. innuptus*, *P. leucopterus*, *P. piercei piercei*, *P. renimaculatus*, *P. simulans*, *Svastra machaerantherae*, *S. obliqua*, *Syntrichalonia exquisita*, *Triepeolus cyclurus*, *T. dacotensis*
- Helianthus pumilus*: *Heteranthidium zebratum*, *Melissodes agilis*
- Helianthus radula*: *Andrena accepta*, *Dufourea marginata*, *Halictus ligatus*, *Heteranthidium zebratum*, *Megachile albitarsis*, *M. mendica*, *M. parallela*, *Melissodes agilis*, *M. dentiventris*, *M. rustica*, *Nomia heteropoda*, *Perdita bequaerti*, *Pseudopanurgus rugosus*, *Svastra aegis*, *S. texana*
- Helianthus rigidus*: *Andrena accepta*, *A. chromotricha*, *A. helianthi*, *Bombus fraternus*, *B. griseocollis*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *Dialictus pilosus pilosus*, *D. versatus*, *Dufourea marginata*, *Evyllaenus pectoralis*, *Halictus ligatus*, *Hesperapis carinata*, *Heteranthidium zebratum*, *Megachile brevis*, *M. fortis*, *M. inimica*, *M. latimanus*, *Melissodes agilis*, *M. coloradensis*, *M. snowii*, *Perdita albipennis*, *P. dolichocephala*, *P. tridentata*, *Psithyrus variabilis*, *Pterosarus innuptus*, *P. piercei piercei*, *Svastra obliqua*, *Triepeolus concavus*
- Helianthus salicifolius*: *Andrena accepta*, *Melissodes agilis*, *M. coreopsis*, *M. trinodis*
- Helianthus strumosus*: *Agapostemon sericeus*, *Andrena accepta*, *A. aliciae*, *A. chromotricha*, *A. helianthi*, *A. peckhami*, *Apis mellifera*, *Augochlorella striata*, *Augochloropsis metallica metallica*, *Bombus centralis*, *B. griseocollis*, *B. pennsylvanicus pennsylvanicus*, *B. ternarius*, *B. terricola*, *B. vagans vagans*, *Calliopsis andreniformis*, *Ceratina dupla*, *Coelioxys funeraria*, *C. modesta*, *C. octodentata*, *C. sodalis*, *C. rufitarsus*, *C. sayi*, *C. texana*, *Dialictus albipennis*, *Evyllaenus pectoralis*, *Halictus confusus*, *H. rubicundus*, *Heriades carinata*, *Hoplitis cylindrica*, *H. simplex*, *Lasioglossum coriaceum*, *Megachile brevis*, *M. centuncularis*, *M. latimanus*, *M. mendica*, *M. petulans*, *M. pugnata pugnata*, *Melissodes agilis*, *M. desponsa*,

M. illata, *M. rustica*, *M. trinodis*, *Nomada graenicheri*, *N. vincta vincta*, *Paranthidium jugatorum*, *Psithyrus citrinus*, *Pterosarus innuptyus*, *P. labrosiformis labrosiformis*, *Svastra obliqua*, *Triepeolus concavus*, *T. cressonii cressonii*, *T. donatus*, *T. pectoralis*

Helianthus tuberosus: *Andrena accepta*, *A. aliciae*, *A. chromotricha*, *A. helianthi*, *A. simplex*, *Augochlorella striata*, *Bombus griseocolis*, *B. nevadensis*, *B. pennsylvanicus pennsylvanicus*, *B. vagans vagans*, *Colletes compactus*, *Dufourea marginata*, *Dialictus imitatus*, *D. pilosus pilosus*, *D. zephyrus*, *Epeolus autumnalis*, *Evylaeus pectinatus*, *E. pectoralis*, *Halictus ligatus*, *Lasioglossum coriaceum*, *Megachile albitarsis*, *M. brevis*, *M. inimica*, *M. latimanus*, *M. pugnata pugnata*, *Melissodes agilis*, *M. bidentis*, *M. bimaculata bimaculata*, *M. boltoniae*, *M. coloradensis*, *M. coreopsis*, *M. rustica*, *M. trinodis*, *M. vernoniae*, *Nomada vincta vincta*, *Pseudopanurgus rugosus*, *Pterosarus innuptyus*, *P. labrosiformis labrosiformis*, *P. labrosus*, *P. piercei piercei*, *P. solidaginis*, *Svastra obliqua*, *Triepeolus concavus*, *T. lunatus*

While we are able to provide lists of bees for 24 North American species of *Helianthus* from all the sections and series recognized by Heiser et al. (1969), there is no information on bees available for the following species of *Helianthus*:

Section Annui: *H. agrestis*, *H. anomalus*, *H. argophyllus*, *H. deserticola*, *H. neglectus*, *H. paradoxus*, *H. praecox*, *H. similis*,
Section Ciliares
Series Pumili: *H. cusickii*
Series Ciliares: *H. arizonensis*, *H. laciniatus*
Section Divaricati
Series Divaricati: *H. decapetalus*, *H. eggerti*, *H. hirsutus*
Series Gigantei: *H. californicus*, *H. resinosus*, *H. schweinitzii*
Series Microcephali: *H. glaucophyllus*, *H. laevigatus*, *H. longifolius*, *H. smithii*
Series Angustifolii: *H. floridanus*, *H. simulans*
Series Atrorubentes: *H. carnosus*, *H. heterophyllus*, *H. silphoides*

Geographic Relationships of Bees Associated with *Helianthus*

In an attempt to learn something about the geographic relationships of the bees associated with *Helianthus*, the following listings of the oligoleges of Compositae primarily associated with *Helianthus* are presented in terms of their geographic occurrence in North America. For this purpose we have selected eight regions that are allopatric and possess rather distinctively different climates. These are Eastern North America, Texas Gulf Coast, Great Plains, Great Basin, Chihuahuan Desert, Sonoran Desert, Mojave

Desert, and Cismontane Pacific Coast. Each of these regions is generally understood by biologists and each to some extent possesses a rather distinctive fauna of bees. Even so it should be kept in mind that some regions such as the adjacent Chihuahuan and Sonoran Deserts are more alike climatically than are the Great Basin and Eastern North America.

The regional relationships of the oligoleges of Compositae primarily associated with *Helianthus* are presented in Figure 1 and their relationships with the various species of *Helianthus* are summarized in Table N.

1. Species generally distributed throughout the range of *Helianthus* in North America (occupying all 8 geographic regions):

Megachile parallela
Melissodes agilis
Svastra obliqua

2. Species widely distributed within the range of *Helianthus* in North America (occupying 4, 5, or 6 geographic regions):

Andrena accepta: Eastern North America, Great Plains, Great Basin, Chihuahuan Desert, Sonoran Desert
Andrena helianthi: Eastern North America, Great Plains, Chihuahuan Desert, Great Basin
Diadasia enavata: Great Plains, Chihuahuan Desert, Sonoran Desert, Mojave Desert, Great Basin, Cismontane Pacific Coast
Nomia heteropoda: Eastern North America, Texas Gulf Coast, Great Plains, Great Basin, Chihuahuan Desert, Sonoran Desert

3. Species restricted to 3 geographic regions within the range of *Helianthus* in North America:

Dufourea marginata: Great Plains, Great Basin, Chihuahuan Desert
Melissodes coloradensis: Eastern North America, Great Plains, Great Basin
Nomia triangulifera: Great Plains, Great Basin, Chihuahuan Desert
Perdita albipennis: Great Plains, Great Basin, Chihuahuan Desert
Perdita lingualis: Great Plains, Great Basin, Chihuahuan Desert
Pseudopanurgus aethiops: Great Plains, Great Basin, Chihuahuan Desert
Pterosarus innuptyus: Great Plains, Great Basin, Chihuahuan Desert

Svastra helianthelli: Great Plains, Chihuahuan Desert, Sonoran Desert

4. Species restricted to 2 geographic regions within the range of *Helianthus* in North America:

Andrena aliciae: Eastern North America, Great Plains
Hesperapis carinata: Great Plains, Great Basin
Heteranthidium occidentale: Great Plains, Chihuahuan Desert
Heteranthidium zebratum: Great Plains, Chihuahuan Desert
Melissodes coreopsis: Great Plains, Chihuahuan Desert
Melissodes perlusa: Great Plains, Great Basin
Melissodes robustior: Great Basin, Cismontane Pacific Coast
Melissodes trinodis: Eastern North America, Great Plains
Pseudopanurgus rugosus: Eastern North America, Great Plains
Svastra machaerantherae: Chihuahuan Desert, Sonoran Desert

5. Species restricted to a single geographic region within the range of *Helianthus* in North America:

Andrena haynesi: Great Plains
Andrena peckhami: Eastern North America
Exomalopsis pygmaea: Great Plains
Heteranthidium cordaticeps: Chihuahuan Desert
Melissodes gelida: Great Plains
Nomia micheneri: Chihuahuan Desert
Perdita bequaerti: Eastern North America
Perdita laticincta: Great Plains
Perdita scopata: Texas Gulf Coast
Perdita tricincta: Texas Gulf Coast
Perdita tridentata: Great Plains
Pterosarus helianthi: Great Plains
Pterosarus piercei piercei: Great Plains
Pterosarus simulans: Great Plains

Listed below by geographic regions are the species of oligoleges of Compositae primarily associated with *Helianthus*. In these lists those oligoleges restricted to the geographic region in which they are listed are preceded by an asterisk. In all other cases, the species entry is followed by the other geographic region(s) in which it is known to occur. For convenience the eight recognized geographic regions are arranged alphabetically below.

CHIHUAHUAN DESERT

Andrena accepta: Eastern North America, Great Basin, Great Plains, Sonoran Desert
Andrena helianthi: Eastern North America, Great Basin, Great Plains

Diadasia enavata: Cismontane Pacific Coast, Great Basin, Great Plains, Mojave Desert, Sonoran Desert
Dufourea marginata: Great Basin, Great Plains
 **Heteranthidium cordaticeps*
Heteranthidium occidentale: Great Plains
Heteranthidium zebratum: Great Plains
Megachile parallela: Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes coreopsis: Great Plains
Nomia heteropoda: Eastern North America, Great Basin, Great Plains, Sonoran Desert, Texas Gulf Coast
 **Nomia micheneri*
Nomia triangulifera: Great Basin, Great Plains
Perdita albipennis: Great Basin, Great Plains
Perdita lingualis: Great Basin, Great Plains
Pseudopanurgus aethiops: Great Basin, Great Plains
Pterosarus innuptus: Great Basin, Great Plains
Svastra helianthelli: Great Plains, Sonoran Desert
Svastra machaerantherae: Sonoran Desert
Svastra obliqua: Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast

CISMONTANE PACIFIC COAST

Diadasia enavata: Chihuahuan Desert, Great Basin, Great Plains, Mojave Desert, Sonoran Desert
Megachile parallela: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes robustior: Great Basin
Svastra obliqua: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast

EASTERN NORTH AMERICA

Andrena accepta: Chihuahuan Desert, Great Basin, Great Plains, Sonoran Desert
Andrena aliciae: Great Plains
Andrena helianthi: Chihuahuan Desert, Great Basin, Great Plains
 **Andrena peckhami*
Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes coloradensis: Great Basin, Great Plains

Melissodes trinodis: Great Plains
Nomia heteropoda: Chihuahuan Desert, Great Basin, Great Plains, Sonoran Desert, Texas Gulf Coast
 * *Perdita bequaerti*
Pseudopanurgus rugosus: Great Plains
Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast

GREAT BASIN

Andrena accepta: Chihuahuan Desert, Eastern North America, Great Plains, Sonoran Desert
Andrena helianthi: Chihuahuan Desert, Eastern North America, Great Plains
Diadasia enavata: Chihuahuan Desert, Cismontane Pacific Coast, Great Plains, Mojave Desert, Sonoran Desert
Dufourea marginata: Chihuahuan Desert, Great Plains
Hesperapis carinata: Great Plains
Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes coloradensis: Eastern North America, Great Plains
Melissodes perlusa: Great Plains
Melissodes robustior: Cismontane Pacific Coast
Nomia heteropoda: Chihuahuan Desert, Eastern North America, Great Plains, Sonoran Desert, Texas Gulf Coast
Nomia triangulifera: Chihuahuan Desert, Great Plains
Perdita albipennis: Chihuahuan Desert, Great Plains
Perdita lingualis: Chihuahuan Desert, Great Plains
Pseudopanurgus aethiops: Chihuahuan Desert, Great Plains
Pterosarus innuptus: Chihuahuan Desert, Great Plains
Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Plains, Mojave Desert, Sonoran Desert, Texas Gulf Coast

GREAT PLAINS

Andrena accepta: Chihuahuan Desert, Eastern North America, Great Basin, Sonoran Desert
Andrena aliciae: Eastern North America
 * *Andrena haynesi*
Andrena helianthi: Chihuahuan Desert, Eastern North America, Great Basin
Diadasia enavata: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Mojave Desert, Sonoran Desert
Dufourea marginata: Chihuahuan Desert, Great Basin
 * *Exomalopsis pygmaea*
Hesperapis carinata: Great Basin
Heteranthidium occidentale: Chihuahuan Desert
Heteranthidium zebratum: Chihuahuan Desert
Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Mojave

Desert, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Mojave Desert, Sonoran Desert, Texas Gulf Coast
Melissodes coloradensis: Eastern North America, Great Basin
Melissodes coreopsis: Chihuahuan Desert
 * *Melissodes gelida*
Melissodes perlusa: Great Basin
Melissodes trinodis: Eastern North America
Nomia heteropoda: Chihuahuan Desert, Eastern North America, Great Basin, Sonoran Desert, Texas Gulf Coast
Nomia triangulifera: Chihuahuan Desert, Great Basin
Perdita albipennis: Chihuahuan Desert, Great Basin
 * *Perdita laticincta*
Perdita lingualis: Chihuahuan Desert, Great Basin
 * *Perdita simulans*
 * *Perdita tridentata*
Pseudopanurgus aethiops: Chihuahuan Desert, Eastern North America, Great Basin
Pseudopanurgus rugosus: Eastern North America
 * *Pterosarus helianthi*
Pterosarus innuptus: Chihuahuan Desert, Great Basin
 * *Pterosarus piercei piercei*
Svastra helianthelli: Chihuahuan Desert, Sonoran Desert
Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Mojave Desert, Sonoran Desert, Texas Gulf Coast

MOJAVE DESERT

Diadasia enavata: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Great Plains, Sonoran Desert
Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Sonoran Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Sonoran Desert, Texas Gulf Coast
Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Sonoran Desert, Texas Gulf Coast

SONORAN DESERT

Andrena accepta: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains
Diadasia enavata: Chihuahuan Desert, Cismontane Pacific Coast, Great Basin, Great Plains, Mojave Desert
Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Texas Gulf Coast
Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Texas Gulf Coast
Nomia heteropoda: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains, Texas Gulf Coast
Svastra helianthelli: Chihuahuan Desert, Great Plains

Svastra machaerantherae: Chihuahuan Desert
Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Texas Gulf Coast

TEXAS GULF COAST

Megachile parallela: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert

Melissodes agilis: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert

Nomia heteropoda: Chihuahuan Desert, Eastern North America, Great Basin, Great Plains, Sonoran Desert

* *Perdita scopata*

* *Perdita tricornis*

Svastra obliqua: Chihuahuan Desert, Cismontane Pacific Coast, Eastern North America, Great Basin, Great Plains, Mojave Desert, Sonoran Desert

Geographic Affinities of *Helianthus* Oligoleges and Polyleges

As might be expected, an analysis of the groups of bees associated with *Helianthus* in their various dependent pollen-collecting roles reveals little about their geographic affinities. Furthermore, since species of the genus *Helianthus* in North America occupy various geographic ranges across the United States, southern Canada, and Mexico south into the State of Michoacan, the opportunity exists at present for many different geographically differentiating faunas of bees simultaneously to evolve specialized intrafloral relationships with *Helianthus* under several markedly different climatic regimes. As we have discussed earlier, however, a very high percentage of the pollen-collecting bee fauna associated with *Helianthus* in North America represents oligoleges of the family Compositae. No less than 46 percent of these Compositae oligoleges are either primarily dependent upon the pollen and nectar of *Helianthus* (14 percent) or are secondarily so (32 percent). Thus an analysis of the geographic affinities of the 39 species of those oligoleges primarily associated with *Helianthus* (Table N) seems not only appropriate, but essential to achieve an understanding of the evolutionary history of this bee-flower relationship.

Less than one-third of the 39 oligoleges of

Compositae primarily associated with *Helianthus* belong to genera of Holarctic or greater Old World distribution including *Andrena* (5 species), *Dufourea* (1 species), *Hesperapis* (1 species), *Megachile* (1 species) and *Nomia* (3 species). It is probably significant that many species in the first four of these genera have repeatedly evolved oligolectic relationships with the flora both in the Old and New Worlds. All five of these genera either evolved in the Old World and subsequently invaded the Western Hemisphere (*Dufourea*, *Hesperapis*, *Megachile*) or have an ancient origin at a time when the northern continents were still in contact (*Andrena*, *Nomia*). Since *Megachile* and *Nomia* occur on all continents, each may have invaded the New World more than once and over different routes. *Dufourea*, *Hesperapis*, and *Andrena*, on the other hand, seem to have migrated from the Old World to the New only by northern land routes and, perhaps, more than once. *Andrena*, although an Holarctic genus, should be associated with New World genera when discussing primary oligoleges of *Helianthus*, since all five species of *Andrena* associated with sunflowers are members of subgenera (*Callandrena* and *Cnemidandrena*) that arose in the New World (LaBerge, 1967, Donovan, 1977) and are restricted to the New World (*Callandrena*) or occur primarily here (*Cnemidandrena*).

It is noteworthy that the very large and diverse genus *Megachile* contains only one species (*M. parallela*) that has established a primary relationship with *Helianthus*, even though a number are oligoleges of Compositae. Similar comments also apply to the other genera just discussed, except *Andrena*.

It is significant that the genera of Holarctic or greater Old World distribution (excepting *Andrena*) number only one-fifth (6) of the primary oligoleges attached to *Helianthus*, and that four-fifths (24) of such species belong to genera or subgenera (in the case of *Andrena*) that evolved in the New World and are found only or primarily here. Most of these genera are either present only in North America (*Heteranthidium*, *Perdita*, *Pseudopanurgus*, *Pterosarus*, *Andrena*) or are most diverse and numerous on this continent even though they

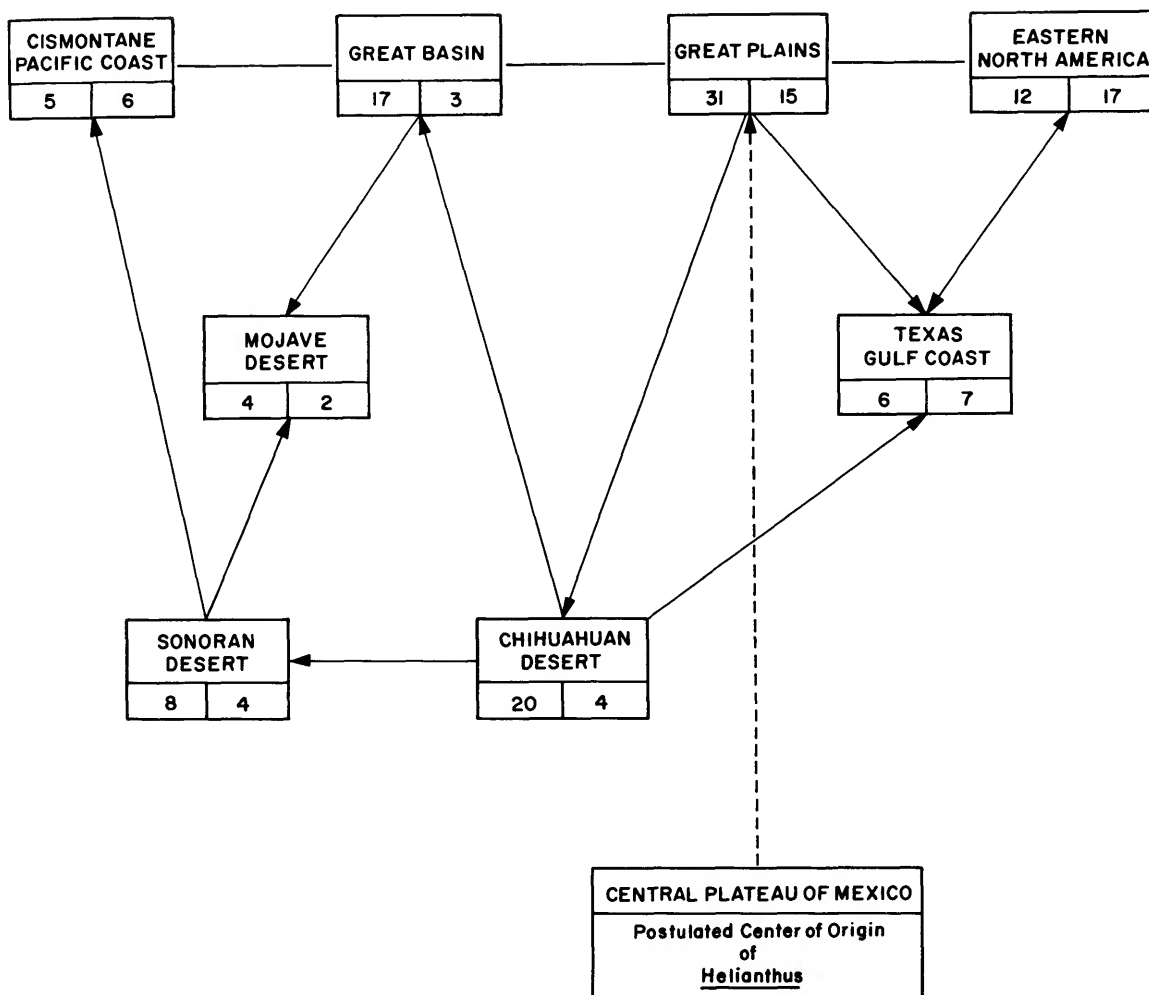


FIGURE 1.—Regional relationships of the oligoleges of Compositae primarily associated with *Helianthus*. (Arrows indicate probable main avenues of derivation and differentiation of these oligoleges following the presumed origin of this bee-flower relationship; numbers in boxes refer to number of bee taxa (on left) and number of *Helianthus* species (on right) involved in each of the regional relationships; drawn by Celeste Green, Department of Entomological Sciences, University of California, Berkeley.)

are also represented in South America (*Diadasia*, *Exomalopsis*, *Melissodes*, and *Svastra*). In view of this we conclude that these are the genera or subgenera of bees that established the initial relationship with *Helianthus* and that only later in the evolutionary history of this bee-flower relationship did the invading genera from the Old World (viz., *Dufourea*, *Hesperapis*, *Megachile*, and

Nomia) establish their relationships with *Helianthus*. This not only seems to explain their fewer numbers in relation to the species of *Helianthus*, but also suggests that the center of origin for the genus and its initially associated bee fauna was located to the south of its present center of distribution in North America, probably in the area of the Mexican Plateau (Figure 1).

Seasonal Occurrence of Bees Associated with *Helianthus*

In the northern tier of states (e.g., Wisconsin, see Graenicher, 1909) where the species of *Helianthus* mostly bloom in July, August, and September (*H. grosseserratus* somewhat later), most of the bee visitors (oligoleges, casuals, and nectar seekers) are active during this time. In fact, throughout the range of the genus, even in the southern regions, by far the majority of visitors are bees of the summer and fall (including such primary oligoleges as *Megachile parallela*).

Among the solitary bees, the most widespread species (e.g., *Svastra obliqua* and *M. agilis*) have the longest flight periods, which in the more southern parts of their ranges may cover the period June to November; the same is true of *Diadasia enavata* in the Southwest. Presumably these species have multiple or overlapping broods. The eusocial bees (e.g., *Apis*, *Bombus*) and primitively eusocial bees (e.g., *Halictus*, especially *H. ligatus*) are in flight throughout the sunflower season, in both the northern and southern regions.

In areas where sunflower blooms early, as along the Pacific Coast and in the southeast and southwest, early season bees such as the species of *Osmia* which fly in March, April, and May avail themselves of the nectar or pollen.

Diurnal Patterns of Pollen Collecting

Although weather conditions, the mixture of species of pollen-collecting bees at a given site, and the size (and thus relative competitive advantage) of the local population affect the diurnal patterns of pollen collection in bees that exploit the flowers of *Helianthus*, when a sufficient number of samples are available to minimize or eliminate these variables, it is clear that several patterns of behavior are involved. These are essentially similar to the patterns described by Hurd and Linsley (1975) for visitors to the creosote bush, *Larrea tridentata*, a desert plant that likewise has pollen and nectar available throughout the day.

Our field sampling data, recorded in Tables A-

M and supplemented in the species accounts, suggest a number of generalizations, of which a few may be selected for special emphasis. Unlike *Larrea*, which makes pollen available before dawn, the *Helianthus* species with which we have worked do not do so until sunrise or shortly afterward. We have seen pollen-seeking females cruising flowers or sipping nectar before anthesis, but, in general, they arrive to coincide with anthesis.

Other things being equal, the first pollen-collecting females to reach the flowers are such primary oligoleges as *Melissodes agilis* (Tables B-H, J-M), *Nomia heteropoda* (Tables C, D, F) and *Diadasia enavata* (Tables I-K, M), when abundant, although they may arrive somewhat later under intense competition. *Melissodes agilis*, however, under favorable conditions, collects pollen primarily for the first two or three hours after sunrise and returns at a comparable period before sunset, with scattered nectar-seekers and even pollen-collectors in the interim. *Nomia heteropoda*, *Diadasia enavata*, and the regular polylege *Halictus ligatus*, also start early when pollen is abundant but continue throughout the day as long as pollen is available although successive pollen loads become smaller and smaller. *Bombus pennsylvanicus sonorus* (Tables D, E) may sometimes start early, but may also concentrate in the middle of the day (Tables G, L).

Other all-day pollen-collectors that tend to concentrate in the early morning are *Andrena accepta* (Tables B, G), *Svastra machaerantherae* (Tables B-D), and *S. obliqua* (Tables B, C, K, L) to name a few. On the other hand, *Megachile parallela* (Tables A-C), an all-day pollen-seeker, tends to be more abundant in the afternoon.

Parasitic bees, presumably seeking the burrows of their hosts in the morning, as well as throughout the period of host activity, tend to be most abundant at sunflowers from midmorning to late afternoon.

Species Accounts

In the discussions that follow, the species are arranged in the phylogenetic sequence of the recently published "Superfamily Apoidea"

(Hurd, 1979) in *Catalog of Hymenoptera in America North of Mexico*. Each species is classed on the basis of intrafloral relationship according to the criteria set forth in the section "Intrafloral Relationships of Bees Associated with *Helianthus*" herein. The list contains 131 oligoleges (39 primary oligoleges, 92 secondary oligoleges), 153 polyleges (22 regular polyleges, 131 casual polyleges), 72 nectar-seeking species not known to take pollen from these flowers, and 56 parasitic species. Doubtless additional species will be discovered to visit these flowers in North America, particularly when detailed investigations are undertaken in those regions not specially emphasized in this study.

COLLETIDAE

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|-------------------------------------|---------------------|
| 1. <i>Colletes americanus</i> | nectar visitor |
| 2. <i>Colletes compactus</i> | secondary oligolege |
| 3. <i>Colletes fulgidus</i> | casual polylege |
| 4. <i>Colletes louisae</i> | nectar visitor |
| 5. <i>Colletes perileucus</i> | nectar visitor |
| 6. <i>Colletes rufocinctus</i> | secondary oligolege |
| 7. <i>Colletes simulans armatus</i> | secondary oligolege |
| 8. <i>Colletes susannae</i> | secondary oligolege |
| 9. <i>Colletes wootoni</i> | nectar visitor |

OXAEIDAE

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|------------------------------|----------------|
| 1. <i>Protoxaea gloriosa</i> | nectar visitor |
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ANDRENIDAE

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| 1. <i>Andrena (Callandrena) accepta</i> | primary oligolege |
| 2. <i>Andrena (Callandrena) aliciae</i> | primary oligolege |
| 3. <i>Andrena (Callandrena) duplicata</i> | secondary oligolege |
| 4. <i>Andrena (Callandrena) haynesi</i> | primary oligolege |
| 5. <i>Andrena (Callandrena) helianthi</i> | primary oligolege |
| 6. <i>Andrena (Callandrena) pecosana</i> | secondary oligolege |
| 7. <i>Andrena (Callandrena) simplex</i> | secondary oligolege |
| 8. <i>Andrena (Cnemidandrena) chromotricha</i> | secondary oligolege |
| 9. <i>Andrena (Cnemidandrena) peckhami</i> | primary oligolege |
| 10. <i>Andrena (Euandrena) lawrencei</i> | casual polylege |
| 11. <i>Andrena (Leucandrena) recta</i> | casual polylege |
| 12. <i>Andrena (Micrandrena) microchlora</i> | casual polylege |
| 13. <i>Andrena (Plastandrena) prunorum</i> | casual polylege |
| 14. <i>Andrena (Simandrena) pallidifovea</i> | secondary oligolege |
| 15. <i>Protandrena bancrofti</i> | casual polylege |
| 16. <i>Protandrena mexicanorum</i> | nectar visitor |
| 17. <i>Pseudopanurgus aethiops</i> | primary oligolege |
| 18. <i>Pseudopanurgus rugosus</i> | primary oligolege |
| 19. <i>Pterosarus albitarsis</i> | secondary oligolege |
| 20. <i>Pterosarus expallidus</i> | nectar visitor |
| 21. <i>Pterosarus helianthi</i> | primary oligolege |
| 22. <i>Pterosarus inuuptus</i> | primary oligolege |

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| 23. <i>Pterosarus labrosiformis labrosiformis</i> | secondary oligolege |
| 24. <i>Pterosarus labrosus</i> | secondary oligolege |
| 25. <i>Pterosarus leucopterus</i> | nectar visitor |
| 26. <i>Pterosarus occiduus</i> | secondary oligolege |
| 27. <i>Pterosarus perlaevis</i> | secondary oligolege |
| 28. <i>Pterosarus piercei piercei</i> | primary oligolege |
| 29. <i>Pterosarus renimaculatus</i> | secondary oligolege |
| 30. <i>Pterosarus rudbeckiae</i> | secondary oligolege |
| 31. <i>Pterosarus simulans</i> | primary oligolege |
| 32. <i>Pterosarus solidaginis</i> | secondary oligolege |
| 33. <i>Pterosarus stigmalis</i> | secondary oligolege |
| 34. <i>Metapsaenythia abdominalis abdominalis</i> | nectar visitor |
| 35. <i>Nomadopsis (Micronomadopsis) helianthi</i> | nectar visitor |
| 36. <i>Calliopsis (Calliopsis) andreniformis</i> | nectar visitor |
| 37. <i>Calliopsis (Calliopsima) crypta</i> | secondary oligolege |
| 38. <i>Calliopsis (Calliopsima) pectidis</i> | secondary oligolege |
| 39. <i>Calliopsis (Calliopsima) pugionis</i> | secondary oligolege |
| 40. <i>Calliopsis (Calliopsima) rozemi</i> | secondary oligolege |
| 41. <i>Perdita (Cockerellia) albipennis</i> | primary oligolege |
| 42. <i>Perdita (Cockerellia) bequaerti</i> | primary oligolege |
| 43. <i>Perdita (Cockerellia) lingualis</i> | primary oligolege |
| 44. <i>Perdita (Cockerellia) scopata</i> | primary oligolege |
| 45. <i>Perdita (Cockerellia) tricineta</i> | primary oligolege |
| 46. <i>Perdita (Cockerellia) verbesinae</i> | secondary oligolege |
| 47. <i>Perdita (Hexaperdita) alexi</i> | secondary oligolege |
| 48. <i>Perdita (Hexaperdita) ignota crawfordi</i> | secondary oligolege |
| 49. <i>Perdita (Hexaperdita) pratti</i> | secondary oligolege |
| 50. <i>Perdita (Hexaperdita) xanthisma</i> | secondary oligolege |
| 51. <i>Perdita (Pentaperdita) nigroviridis</i> | secondary oligolege |
| 52. <i>Perdita (Perdita) affinis</i> | secondary oligolege |
| 53. <i>Perdita (Perdita) aridella</i> | secondary oligolege |
| 54. <i>Perdita (Perdita) bruneri</i> | secondary oligolege |
| 55. <i>Perdita (Perdita) dolichocephala</i> | secondary oligolege |
| 56. <i>Perdita (Perdita) fallax</i> | secondary oligolege |
| 57. <i>Perdita (Perdita) gerhardi dallasiana</i> | casual polylege |
| 58. <i>Perdita (Perdita) laticincta</i> | primary oligolege |
| 59. <i>Perdita (Perdita) prionopsidis</i> | secondary oligolege |
| 60. <i>Perdita (Perdita) swenki</i> | secondary oligolege |
| 61. <i>Perdita (Perdita) tridentata</i> | primary oligolege |
| 62. <i>Perdita (Perdita) zebata zebata</i> | nectar visitor |
| 63. <i>Perdita (Pygoperdita) nebrascensis</i> | secondary oligolege |

HALICTIDAE

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| 1. <i>Dufourea (Halictoides) marginata</i> | primary oligolege |
| 2. <i>Nomia (Curvinomia) angustitibialis</i> | nectar visitor |
| 3. <i>Nomia (Curvinomia) fedorensis</i> | nectar visitor |
| 4. <i>Nomia (Curvinomia) mesillensis</i> | nectar visitor |
| 5. <i>Nomia (Acunomia) nortoni nortoni</i> | casual polylege |
| 6. <i>Nomia (Acunomia) melanderi</i> | nectar visitor |

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| 7. <i>Nomia (Epinomia) micheneri</i> | primary oligolege | 58. <i>Dialictus pilosus pilosus</i> | casual polylege |
| 8. <i>Nomia (Epinomia) nevadensis angelisia</i> | nectar visitor | 59. <i>Dialictus pruinosiformis</i> | casual polylege |
| 9. <i>Nomia (Epinomia) nevadensis arizonensis</i> | nectar visitor | 60. <i>Dialictus punctatoventris</i> | casual polylege |
| 10. <i>Nomia (Epinomia) triangulifera</i> | primary oligolege | 61. <i>Dialictus tegulariformis</i> | casual polylege |
| 11. <i>Nomia (Dieunomia) apache</i> | secondary oligolege | 62. <i>Dialictus veganus</i> | casual polylege |
| 12. <i>Nomia (Dieunomia) bolliana</i> | secondary oligolege | 63. <i>Dialictus versatus</i> | casual polylege |
| 13. <i>Nomia (Dieunomia) heteropoda</i> | primary oligolege | 64. <i>Dialictus zephyrus</i> | casual polylege |
| 14. <i>Augochloropsis (Paraugochloropsis) metallica metallica</i> | casual polylege | 65. <i>Sphecodes dichrous</i> | cleptoparasite |
| 15. <i>Augochloropsis (Paraugochloropsis) sumptuosa</i> | casual polylege | MELITTIDAE | |
| 16. <i>Augochlora (Augochlora) pura</i> | casual polylege | 1. <i>Hesperapis (Panurgomia) arenicola</i> | secondary oligolege |
| 17. <i>Augochlorella aurata</i> | casual polylege | 2. <i>Hesperapis (Panurgomia) carinata</i> | primary oligolege |
| 18. <i>Augochlorella bracteata</i> | casual polylege | MEGACHILIDAE | |
| 19. <i>Augochlorella gratioiosa</i> | casual polylege | 1. <i>Lithurge (Lithurgopsis) gibbosus</i> | nectar visitor |
| 20. <i>Augochlorella persimilis</i> | casual polylege | 2. <i>Heteranthidium cordaticeps</i> | primary oligolege |
| 21. <i>Augochlorella pomoniella</i> | nectar visitor | 3. <i>Heteranthidium occidentale</i> | primary oligolege |
| 22. <i>Augochlorella striata</i> | casual polylege | 4. <i>Heteranthidium timberlakei</i> | secondary oligolege |
| 23. <i>Agapostemon angelicus</i> | casual polylege | 5. <i>Heteranthidium zebratum</i> | primary oligolege |
| 24. <i>Agapostemon cockerelli</i> | casual polylege | 6. <i>Paranthidium (Paranthidium) jugatorium</i> | secondary oligolege |
| 25. <i>Agapostemon femoratus</i> | casual polylege | 7. <i>Anthidium (Anthidium) maculosum</i> | nectar visitor |
| 26. <i>Agapostemon melliventris</i> | casual polylege | 8. <i>Anthidium (Anthidium) paroselae</i> | casual polylege |
| 27. <i>Agapostemon sericeus</i> | casual polylege | 9. <i>Anthidium (Anthidium) porterae</i> | nectar visitor |
| 28. <i>Agapostemon splendens</i> | casual polylege | 10. <i>Callanthidium illustre</i> | casual polylege |
| 29. <i>Agapostemon texanus</i> | regular polylege | 11. <i>Dianthidium curvatum sayi</i> | secondary oligolege |
| 30. <i>Agapostemon tyleri</i> | casual polylege | 12. <i>Dianthidium dubium dilectum</i> | casual polylege |
| 31. <i>Agapostemon virescens</i> | casual polylege | 13. <i>Dianthidium ulkei</i> | casual polylege |
| 32. <i>Halictus (Halictus) farinosus</i> | casual polylege | 14. <i>Anthidiellum notatum notatum</i> | casual polylege |
| 33. <i>Halictus (Halictus) ligatus</i> | regular polylege | 15. <i>Anthidiellum perplexum</i> | casual polylege |
| 34. <i>Halictus (Halictus) rubicundus</i> | casual polylege | 16. <i>Dioxys aurifuscus</i> | cleptoparasite |
| 35. <i>Halictus (Seladonia) confusus</i> | casual polylege | 17. <i>Dioxys pomonae pomonae</i> | cleptoparasite |
| 36. <i>Halictus (Seladonia) tripartitus</i> | casual polylege | 18. <i>Heriades (Neotrypetes) variolosa variolosa</i> | regular polylege |
| 37. <i>Lasioglossum coriaceum</i> | casual polylege | 19. <i>Heriades (Physostetha) carinata</i> | casual polylege |
| 38. <i>Lasioglossum mellipes</i> | nectar visitor | 20. <i>Heriades (Physostetha) occidentalis</i> | casual polylege |
| 39. <i>Lasioglossum sisymbrii</i> | casual polylege | 21. <i>Chelostomopsis rubifloris</i> | casual polylege |
| 40. <i>Lasioglossum titusi</i> | casual polylege | 22. <i>Hoplitis (Andronicus) cylindrica</i> | casual polylege |
| 41. <i>Evyllaes aberrans</i> | nectar visitor | 23. <i>Hoplitis (Dasyosmia) biscutellae</i> | nectar visitor |
| 42. <i>Evyllaes amicus</i> | nectar visitor | 24. <i>Hoplitis (Alcidamea) pilosifrons</i> | casual polylege |
| 43. <i>Evyllaes argemonis</i> | nectar visitor | 25. <i>Hoplitis (Alcidamea) producta</i> | regular polylege |
| 44. <i>Evyllaes kincaidii</i> | casual polylege | 26. <i>Hoplitis (Alcidamea) sambuci</i> | casual polylege |
| 45. <i>Evyllaes pectinatus</i> | nectar visitor | 27. <i>Hoplitis (Alcidamea) truncata truncata</i> | casual polylege |
| 46. <i>Evyllaes pectoralis</i> | casual polylege | 28. <i>Hoplitis (Robertsonella) simplex</i> | casual polylege |
| 47. <i>Evyllaes pectoraloides</i> | casual polylege | 29. <i>Anthocopa (Eremosmia) hemizoniae</i> | secondary oligolege |
| 48. <i>Dialictus albipennis</i> | nectar visitor | 30. <i>Ashmeadiella (Ashmeadiella) buconis</i> | secondary oligolege |
| 49. <i>Dialictus clematisellus</i> | nectar visitor | 31. <i>Ashmeadiella (Ashmeadiella) californica</i> | secondary oligolege |
| 50. <i>Dialictus illinoensis</i> | nectar visitor | 32. <i>Ashmeadiella (Ashmeadiella) foveata</i> | casual polylege |
| 51. <i>Dialictus imitatus</i> | casual polylege | 33. <i>Ashmeadiella (Ashmeadiella) titusi</i> | nectar visitor |
| 52. <i>Dialictus impavidus</i> | nectar visitor | 34. <i>Osmia (Chalcosmia) coloradensis</i> | secondary oligolege |
| 53. <i>Dialictus incompletus</i> | casual polylege | 35. <i>Osmia (Chalcosmia) texana</i> | secondary oligolege |
| 54. <i>Dialictus marinus</i> | casual polylege | | |
| 55. <i>Dialictus microlepidoides</i> | nectar visitor | | |
| 56. <i>Dialictus nevadensis</i> | casual polylege | | |
| 57. <i>Dialictus oleosus</i> | nectar visitor | | |

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|---|---------------------|---|---------------------|
| 36. <i>Osmia (Cephalosmia) californica</i> | secondary oligolege | 79. <i>Megachile (Sayapis) helianthi</i> | secondary oligolege |
| 37. <i>Osmia (Cephalosmia) grinnelli</i> | casual polylege | 80. <i>Megachile (Sayapis) inimica</i> | secondary oligolege |
| 38. <i>Osmia (Cephalosmia) montana</i> | secondary oligolege | 81. <i>Megachile (Sayapis) polycaris</i> | regular polylege |
| 39. <i>Osmia (Nothosmia) marginata</i> | casual polylege | 82. <i>Megachile (Sayapis) pugnata pugnata</i> | secondary oligolege |
| 40. <i>Osmia (Chenosmia) clarescens</i> | casual polylege | 83. <i>Chalicodoma (Chelostomoides) angelarum</i> | casual polylege |
| 41. <i>Osmia (Diceratosmia) subfasciata subfasciata</i> | casual polylege | 84. <i>Chalicodoma (Chelostomoides) campanulae campanulae</i> | casual polylege |
| 42. <i>Megachile (Litomegachile) brevis</i> | regular polylege | 85. <i>Chalicodoma (Chelostomoides) chilopsidis</i> | nectar visitor |
| 43. <i>Megachile (Litomegachile) coquilletti</i> | casual polylege | 86. <i>Chalicodoma (Chelostomoides) occidentalis</i> | nectar visitor |
| 44. <i>Megachile (Litomegachile) gentilis</i> | nectar visitor | 87. <i>Chalicodoma (Chelostomoides) odontostoma</i> | nectar visitor |
| 45. <i>Megachile (Litomegachile) lippiae</i> | casual polylege | 88. <i>Chalicodoma (Chelostomoides) spinotulata</i> | nectar visitor |
| 46. <i>Megachile (Litomegachile) mendica</i> | casual polylege | 89. <i>Chalicodoma (Chelostomoides) subexilis</i> | nectar visitor |
| 47. <i>Megachile (Litomegachile) texana</i> | casual polylege | 90. <i>Coelioxys (Coelioxys) sodalis</i> | cleptoparasite |
| 48. <i>Megachile (Cressoniella) zapoteca</i> | casual polylege | 91. <i>Coelioxys (Boreocoelioxys) banksi</i> | cleptoparasite |
| 49. <i>Megachile (Megachile) centuncularis</i> | casual polylege | 92. <i>Coelioxys (Boreocoelioxys) moesta</i> | cleptoparasite |
| 50. <i>Megachile (Megachile) inermis</i> | casual polylege | 93. <i>Coelioxys (Boreocoelioxys) novomexicana</i> | cleptoparasite |
| 51. <i>Megachile (Megachile) montivaga</i> | regular polylege | 94. <i>Coelioxys (Boreocoelioxys) octodentata</i> | cleptoparasite |
| 52. <i>Megachile (Megachile) relativa</i> | casual polylege | 95. <i>Coelioxys (Boreocoelioxys) rufitarsus</i> | cleptoparasite |
| 53. <i>Megachile (Eutricharaea) concinna</i> | nectar visitor | 96. <i>Coelioxys (Boreocoelioxys) sayi</i> | cleptoparasite |
| 54. <i>Megachile (Delomegachile) gemula gemula</i> | casual polylege | 97. <i>Coelioxys (Xerocoelioxys) edita</i> | cleptoparasite |
| 55. <i>Megachile (Delomegachile) melanophaea</i> | casual polylege | 98. <i>Coelioxys (Schizocoelioxys) funeraria</i> | cleptoparasite |
| 56. <i>Megachile (Phaenosarus) agustini</i> | casual polylege | 99. <i>Coelioxys (Synocoelioxys) alternata</i> | cleptoparasite |
| 57. <i>Megachile (Phaenosarus) fortis</i> | regular polylege | 100. <i>Coelioxys (Synocoelioxys) texana</i> | cleptoparasite |
| 58. <i>Megachile (Derotropis) xerophila</i> | secondary oligolege | 101. <i>Coelioxys (Neocoelioxys) menthae</i> | cleptoparasite |
| 59. <i>Megachile (Xeromegachile) alata</i> | secondary oligolege | 102. <i>Coelioxys (Glyptocoelioxys) germana</i> | cleptoparasite |
| 60. <i>Megachile (Xeromegachile) casadae</i> | casual polylege | 103. <i>Coelioxys (Cyrtocoelioxys) modesta</i> | cleptoparasite |
| 61. <i>Megachile (Xeromegachile) coloradensis</i> | nectar visitor | | |
| 62. <i>Megachile (Xeromegachile) dakotensis</i> | secondary oligolege | | |
| 63. <i>Megachile (Xeromegachile) manifesta</i> | secondary oligolege | | |
| 64. <i>Megachile (Xeromegachile) nevadensis</i> | nectar visitor | | |
| 65. <i>Megachile (Argyropile) mucorosa</i> | casual polylege | | |
| 66. <i>Megachile (Argyropile) parallela</i> | primary oligolege | | |
| 67. <i>Megachile (Argyropile) sabinensis</i> | secondary oligolege | | |
| 68. <i>Megachile (Argyropile) townsendiana</i> | casual oligolege | | |
| 69. <i>Megachile (Xanthosarus) dentitarsus</i> | casual polylege | | |
| 70. <i>Megachile (Xanthosarus) latimanus</i> | casual polylege | | |
| 71. <i>Megachile (Xanthosarus) perihirta</i> | regular polylege | | |
| 72. <i>Megachile (Leptorachis) petulans</i> | casual polylege | | |
| 73. <i>Megachile (Pseudocentron) pruina pruina</i> | casual polylege | | |
| 74. <i>Megachile (Pseudocentron) sidalceae</i> | nectar visitor | | |
| 75. <i>Megachile (Acentron) albitarsis</i> | casual polylege | | |
| 76. <i>Megachile (Melanosarus) xylocopoides</i> | casual polylege | | |
| 77. <i>Megachile (Sayapis) fidelis</i> | regular polylege | | |
| 78. <i>Megachile (Sayapis) frugalis</i> | casual polylege | | |

ANTHOPHORIDAE

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| 1. <i>Neolarra helianthi</i> | cleptoparasite |
| 2. <i>Neolarra verbesinae</i> | cleptoparasite |
| 3. <i>Holcopasites heliopsis</i> | cleptoparasite |
| 4. <i>Epeolus autumnalis</i> | cleptoparasite |
| 5. <i>Epeolus bifasciatus</i> | cleptoparasite |
| 6. <i>Epeolus compactus</i> | cleptoparasite |
| 7. <i>Epeolus pusillus</i> | cleptoparasite |
| 8. <i>Triepeolus concavus</i> | cleptoparasite |
| 9. <i>Triepeolus cressonii cressonii</i> | cleptoparasite |
| 10. <i>Triepeolus cyclurus</i> | cleptoparasite |
| 11. <i>Triepeolus dacotensis</i> | cleptoparasite |
| 12. <i>Triepeolus donatus</i> | cleptoparasite |
| 13. <i>Triepeolus helianthi</i> | cleptoparasite |
| 14. <i>Triepeolus lestes</i> | cleptoparasite |
| 15. <i>Triepeolus lineatulus</i> | cleptoparasite |
| 16. <i>Triepeolus lunatus</i> | cleptoparasite |
| 17. <i>Triepeolus nevadensis</i> | cleptoparasite |
| 18. <i>Triepeolus norae</i> | cleptoparasite |

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| 19. <i>Triepeolus pectoralis</i> | cleptoparasite | 66. <i>Melissodes (Melissodes) comptoides</i> | regular polylege |
| 20. <i>Triepeolus rectangularis</i> | cleptoparasite | 67. <i>Melissodes (Melissodes) paroselae</i> | casual polylege |
| 21. <i>Triepeolus remigatus</i> | cleptoparasite | 68. <i>Melissodes (Melissodes) tepida</i> | casual polylege |
| 22. <i>Triepeolus simplex</i> | cleptoparasite | 69. <i>Melissodes (Melissodes) tessellata</i> | regular polylege |
| 23. <i>Triepeolus subnitens</i> | cleptoparasite | 70. <i>Melissodes (Melissodes) thelypodii thelypodii</i> | casual polylege |
| 24. <i>Triepeolus texanus</i> | cleptoparasite | 71. <i>Melissodes (Apomelissodes) fimbriata</i> | nectar visitor |
| 25. <i>Triepeolus trichopygus</i> | cleptoparasite | 72. <i>Melissodes (Heliomelissodes) desponsa</i> | casual polylege |
| 26. <i>Nomada (Heminomada) graenicheri</i> | cleptoparasite | 73. <i>Melissodes (Heliomelissodes) rivalis</i> | secondary oligolege |
| 27. <i>Nomada (Pachynomada) vincta vincta</i> | cleptoparasite | 74. <i>Melissodes (Tachymelissodes) opunttiella</i> | casual polylege |
| 28. <i>Nomada (Micronomada) garciana</i> | cleptoparasite | 75. <i>Melissodes (Tachymelissodes) sonorensis</i> | regular polylege |
| 29. <i>Nomada (Micronomada) gutierreziae</i> | cleptoparasite | 76. <i>Melissodes (Eumelissodes) agilis</i> | primary oligolege |
| 30. <i>Nomada (Micronomada) melanoptera</i> | cleptoparasite | 77. <i>Melissodes (Eumelissodes) appressa</i> | secondary oligolege |
| 31. <i>Nomada (Micronomada) texana</i> | cleptoparasite | 78. <i>Melissodes (Eumelissodes) bidentis</i> | secondary oligolege |
| 32. <i>Nomada (Micronomada) vierecki</i> | cleptoparasite | 79. <i>Melissodes (Eumelissodes) bimatrix</i> | secondary oligolege |
| 33. <i>Paranomada velutina</i> | cleptoparasite | 80. <i>Melissodes (Eumelissodes) boltoniae</i> | regular polylege |
| 34. <i>Exomalopsis (Phanomalopsis) solani</i> | casual polylege | 81. <i>Melissodes (Eumelissodes) brevipygga</i> | secondary oligolege |
| 35. <i>Exomalopsis (Phanomalopsis) solidaginis</i> | casual polylege | 82. <i>Melissodes (Eumelissodes) confusa</i> | secondary oligolege |
| 36. <i>Exomalopsis (Anthophoriscia) morgani</i> | casual polylege | 83. <i>Melissodes (Eumelissodes) coreopsis</i> | primary oligolege |
| 37. <i>Exomalopsis (Anthophoriscia) pygmaea</i> | primary oligolege | 84. <i>Melissodes (Eumelissodes) denticulata</i> | casual polylege |
| 38. <i>Ptilothrix</i> sp. near <i>sumichrasti</i> | nectar visitor | 85. <i>Melissodes (Eumelissodes) dentiventris</i> | secondary oligolege |
| 39. <i>Diadasia afflicta afflicta</i> | nectar visitor | 86. <i>Melissodes (Eumelissodes) gelida</i> | primary oligolege |
| 40. <i>Diadasia australis</i> | nectar visitor | 87. <i>Melissodes (Eumelissodes) grindelliae</i> | secondary oligolege |
| 41. <i>Diadasia bituberculata</i> | nectar visitor | 88. <i>Melissodes (Eumelissodes) humilior</i> | secondary oligolege |
| 42. <i>Diadasia diminuta</i> | nectar visitor | 89. <i>Melissodes (Eumelissodes) illata</i> | secondary oligolege |
| 43. <i>Diadasia enavata</i> | primary oligolege | 90. <i>Melissodes (Eumelissodes) limbus</i> | secondary oligolege |
| 44. <i>Diadasia ochracea</i> | nectar visitor | 91. <i>Melissodes (Eumelissodes) lutulenta</i> | secondary oligolege |
| 45. <i>Diadasia rinconis rinconis</i> | nectar visitor | 92. <i>Melissodes (Eumelissodes) menuachus</i> | secondary oligolege |
| 46. <i>Synhalonia actuosa</i> | casual polylege | 93. <i>Melissodes (Eumelissodes) microsticta</i> | secondary oligolege |
| 47. <i>Synhalonia edwardsii</i> | casual polylege | 94. <i>Melissodes (Eumelissodes) montana</i> | secondary oligolege |
| 48. <i>Syntrichalonia exquisita</i> | secondary oligolege | 95. <i>Melissodes (Eumelissodes) nivea</i> | secondary oligolege |
| 49. <i>Svastra (Brachymelissodes) cressonii</i> | casual polylege | 96. <i>Melissodes (Eumelissodes) pallidifsignata</i> | secondary oligolege |
| 50. <i>Svastra (Epimelissodes) aegis</i> | secondary oligolege | 97. <i>Melissodes (Eumelissodes) paulula</i> | secondary oligolege |
| 51. <i>Svastra (Epimelissodes) atripes atripes</i> | casual polylege | 98. <i>Melissodes (Eumelissodes) perlusa</i> | primary oligolege |
| 52. <i>Svastra (Epimelissodes) grandissima</i> | nectar visitor | 99. <i>Melissodes (Eumelissodes) robustior</i> | primary oligolege |
| 53. <i>Svastra (Epimelissodes) helianthelli</i> | primary oligolege | 100. <i>Melissodes (Eumelissodes) rustica</i> | secondary oligolege |
| 54. <i>Svastra (Epimelissodes) machaerantherae</i> | primary oligolege | 101. <i>Melissodes (Eumelissodes) snowii</i> | secondary oligolege |
| 55. <i>Svastra (Epimelissodes) obliqua</i> | primary oligolege | 102. <i>Melissodes (Eumelissodes) subagilis</i> | secondary oligolege |
| 56. <i>Svastra (Epimelissodes) petulca</i> | secondary oligolege | 103. <i>Melissodes (Eumelissodes) subillata</i> | secondary oligolege |
| 57. <i>Svastra (Epimelissodes) sabinensis</i> | nectar visitor | 104. <i>Melissodes (Eumelissodes) submen-uacha</i> | secondary oligolege |
| 58. <i>Svastra (Epimelissodes) sila</i> | nectar visitor | 105. <i>Melissodes (Eumelissodes) tincta</i> | secondary oligolege |
| 59. <i>Svastra (Epimelissodes) texana</i> | secondary oligolege | 106. <i>Melissodes (Eumelissodes) trinodis</i> | primary oligolege |
| 60. <i>Xenoglossodes bishoppi</i> | nectar visitor | 107. <i>Melissodes (Eumelissodes) tristis</i> | casual polylege |
| 61. <i>Xenoglossodes eriocarpi</i> | nectar visitor | 108. <i>Melissodes (Eumelissodes) velutina</i> | nectar visitor |
| 62. <i>Xenoglossodes helianthorum</i> | nectar visitor | | |
| 63. <i>Peponapis (Peponapis) pruinosae</i> | nectar visitor | | |
| 64. <i>Melissodes (Melissodes) bimaculata bimaculata</i> | regular polylege | | |
| 65. <i>Melissodes (Melissodes) communis communis</i> | regular polylege | | |

109. *Melissodes (Eumelissodes) verbescinarum* nectar visitor
 110. *Melissodes (Eumelissodes) vernoniae* secondary oligolege
 111. *Melissodes (Eumelissodes) wheeleri* secondary oligolege
 112. *Melissodes (Callimelissodes) coloradensis* primary oligolege
 113. *Melissodes (Callimelissodes) composita* secondary oligolege
 114. *Melissodes (Callimelissodes) glenwoodensis* secondary oligolege
 115. *Melissodes (Callimelissodes) lupina* secondary oligolege
 116. *Melissodes (Callimelissodes) lustra* secondary oligolege
 117. *Melissodes (Callimelissodes) plumosa* nectar visitor
 118. *Melissodes (Callimelissodes) stearnsi* secondary oligolege
 119. *Martinapis (Martinapis) occidentalis* nectar visitor
 120. *Anthophora (Anthophora) montana* casual polylege
 121. *Anthophora (Anthophora) smithii* nectar visitor
 122. *Anthophora (Anthophora) urbana urbana* nectar visitor
 123. *Anthophora (Anthophora) walshii* nectar visitor
 124. *Anthophora (Micranthophora) curta* casual polylege
 125. *Anthophora (Micranthophora) maculifrons* casual polylege
 126. *Anthophora (Micranthophora) peritomae* casual polylege
 127. *Xeromelecta (Melectomorpha) californica* cleptoparasite
 128. *Xeromelecta (Melectomorpha) interrupta* cleptoparasite
 129. *Centris (Paracentris) atripes* nectar visitor
 130. *Centris (Paracentris) caesalpiniae* nectar visitor
 131. *Ceratina (Zadontomerus) acantha* casual polylege
 132. *Ceratina (Zadontomerus) apacheorum* casual polylege
 133. *Ceratina (Zadontomerus) calcarata* casual polylege
 134. *Ceratina (Zadontomerus) dupla* casual polylege
 135. *Ceratina (Zadontomerus) micheneri* casual polylege
 136. *Ceratina (Zadontomerus) nanula* casual polylege
 137. *Ceratina (Zadontomerus) neomexicana* casual polylege
 138. *Ceratina (Zadontomerus) pacifica* casual polylege
 139. *Ceratina (Zadontomerus) punctigena* casual polylege
 140. *Ceratina (Zadontomerus) shinnersi* casual polylege
 141. *Ceratina (Zadontomerus) strenua* casual polylege
 142. *Ceratina (Zadontomerus) tejonensis* nectar visitor
 143. *Ceratina (Euceratina) dallatorreana* nectar visitor
 144. *Xylocopa (Xylocopoides) californica* nectar visitor
5. *Bombus (Separatobombus) griseocolis* regular polylege
 6. *Bombus (Separatobombus) morrisoni* regular polylege
 7. *Bombus (Crotchibombus) crotchii* casual polylege
 8. *Bombus (Cullumanobombus) rufocinctus* casual polylege
 9. *Bombus (Pyrobombus) bimaculatus* casual polylege
 10. *Bombus (Pyrobombus) centralis* casual polylege
 11. *Bombus (Pyrobombus) huntii* casual polylege
 12. *Bombus (Pyrobombus) impatiens* casual polylege
 13. *Bombus (Pyrobombus) ternarius* casual polylege
 14. *Bombus (Pyrobombus) vagans vagans* casual polylege
 15. *Bombus (Subterraneobombus) appositus* casual polylege
 16. *Bombus (Subterraneobombus) borealis* casual polylege
 17. *Bombus (Fervidobombus) californicus* casual polylege
 18. *Bombus (Fervidobombus) fervidus fervidus* casual polylege
 19. *Bombus (Fervidobombus) pennsylvanicus pennsylvanicus* regular polylege
 20. *Bombus (Fervidobombus) pennsylvanicus sonorus* regular polylege
 21. *Psithyrus ashtoni* social parasite
 22. *Psithyrus citrinus* social parasite
 23. *Psithyrus insularis* social parasite
 24. *Psithyrus variabilis* social parasite
 25. *Apis mellifera* casual polylege

Family COLLETIDAE

Although this family is represented in America north of Mexico by more than 150 species, only a relatively few species of the genus *Colletes* are known to visit the flowers of *Helianthus*. None of the more than 50 species of *Hylaeus* present in North America has been observed at these flowers. It thus appears that the members of this family are relatively less important as pollinators of *Helianthus* than those of several other families of bees.

Genus *Colletes* Latreille

This is a large genus of bees that is found throughout much of the world except Australia. More than 90 species are known to occur in America north of Mexico (Hurd, 1979) and doubtless other species than those discussed below will be found at the flowers of *Helianthus*. Even so, it seems most unlikely that any additional

APIDAE

1. *Bombus (Bombus) affinis* casual polylege
 2. *Bombus (Bombus) terricola* casual polylege
 3. *Bombus (Fraternobombus) fraternus* regular polylege
 4. *Bombus (Bombias) nevadensis* regular polylege

species will be discovered that have established an oligolectic relationship with this genus of plants.

Nine species of this genus have been found at the flowers of *Helianthus*. Of these, four were seeking nectar only, four have been observed to have established the role of oligoleges secondarily associated with *Helianthus*, and one species (*Colletes fulgidus*) only occasionally takes pollen from the flowers of *Helianthus* and thus is regarded by us as a casual polylege of this plant.

1. *Colletes americanus* Cresson

This species has been reported as a visitor to various Compositae, including nectar-sipping at *Helianthus divaricatus* in Illinois by Robertson (1929). It occurs in southern Canada (Quebec and Manitoba) and the United States, east of the Rocky Mountains to the Atlantic seaboard (Hurd, 1979). Stephen (1954) reports it flying during the fall (August–October) and Mitchell (1960) comments that in Florida males have been collected as early as May.

2. *Colletes compactus* Cresson

The female of *Colletes compactus* proper, an oligolege of the Compositae secondarily associated with *Helianthus*, has been recorded by Robertson (1929) collecting pollen from the flowers of *Helianthus tuberosus* and other Compositae in Illinois. This subspecies ranges from Nova Scotia to Georgia, west to Wisconsin, Missouri, Colorado, and Arizona (Hurd, 1979). It is primarily autumnal in flight (Stephen, 1954), although Mitchell (1960) notes that in the eastern United States it flies from mid-July until mid-November.

3. *Colletes fulgidus* Swenk

The nominate subspecies ranges from British Columbia, Alberta, Montana, and South Dakota, south to California, Nevada, northern Utah, Colorado, Wyoming, and Texas (Hurd, 1979). It flies from May to October, but is most abundant in the summer months (Stephen, 1954). It has been

recorded from flowers of a number of Compositae, but apparently not previously from *Helianthus* and thus is regarded by us as a casual polylege of *H. annuus*.

We have taken it on *Helianthus* as follows:

CALIFORNIA.—TULARE COUNTY: Dinuba, 5.5 mi S, 7 Oct 75, *H. annuus*, 0110-01129, 1♀P (EGL, JML, AEM, MMM).

4. *Colletes louisae* Cockerell

This species ranges through the southwestern deserts from western Texas and adjacent northern Mexico to the Mojave and Colorado Deserts of California and Baja California Norte (Hurd and Linsley, 1975). It is principally an autumnal species visiting Compositae but has a spring flight period in which the females visit desert shrubs as well as composites (Timberlake, 1943). Its relationship with *Helianthus* appears to be that of a nectar visitor (Table C).

5. *Colletes perileucus* Cockerell

This species is apparently active in the spring and early summer. It has been collected primarily at the flowers of *Prosopis* and has been recorded from southern California (Panamint Mountains), Arizona (Cochise County), Texas (Big Bend Park), and Mexico (Baja California and Sonora) by Stephen (1954). It appears to visit the flowers of *Helianthus* only for nectar (Table D).

6. *Colletes rufocinctus* Cockerell

Stevens (1950) has recorded this species from the flowers of *Helianthus petiolaris*, as well as from other Compositae in North Dakota. It ranges from Minnesota west to Alberta, south to South Dakota, Colorado, and Arizona. Stephen (1954) notes that the species is known to be on the wing from 3 August to 15 September. Its relationship with *Helianthus* appears to be that of a secondary oligolege (Table C) since it is known to visit other Compositae, especially *Aster*, *Grindelia*, *Solidago*, and *Taraxacum*.

7. *Colletes simulans armatus* Patton

This subspecies is known to occur on sunflowers in North Dakota (Stevens, 1950) and apparently is an oligolege of autumnal flowering Compositae secondarily associated with *Helianthus*. It ranges from southern Canada (Alberta, Manitoba, Quebec, and Nova Scotia), south into the northern Great Plains states and south to Georgia in the eastern United States (Hurd, 1979). According to Mitchell (1960), this subspecies flies from May to November, and is found in abundance throughout the northern Great Plains to the Atlantic seaboard (Stephen, 1954).

8. *Colletes susannae* Swenk

Colletes susannae, an apparent oligolege of the Compositae secondarily associated with *Helianthus*, visits *H. petiolaris* in North Dakota (Stevens, 1950). It occurs from Illinois, Wisconsin, and Manitoba west to Colorado and Alberta, flying from July 1 to mid-August (Mitchell, 1960).

9. *Colletes wootoni* Cockerell

Colletes wootoni is a common polylectic species, ranging from southern Texas into Arizona. Stephen (1954) lists a wide range of flower records, not including *Helianthus*. Hurd and Linsley (1975) found it to be a regular visitor to *Larrea tridentata* and it apparently only occasionally seeks nectar at the flowers of *Helianthus* (Tables C, D).

Family OXAEIDAE

This is a small family of New World bees that as a group are centered in the tropics (Hurd and Linsley, 1976). Insofar as known, the intrafloral relationships of these bees suggest a rather narrow dependence upon relatively few sources of pollen including only certain genera within the plant families Leguminosae, Solanaceae, and Zygophyllaceae. Both males and females, however, take nectar from a comparatively wide variety of plants since the flowers of some of their preferred pollen sources produce little or no nectar and large quantities of nectar are required to meet the

bioenergetic requirements of these fast-flying bees (Hurd and Linsley, 1976:1).

Two genera of these bees, *Mesoxaea* and *Protoxaea*, are represented within the range of *Helianthus* in North America but only a single species of *Protoxaea* has been taken at the flowers of this plant.

Genus *Protoxaea* Cockerell and Porter

This genus is composed of three species that are found in North America.

1. *Protoxaea gloriosa* (Fox)

The females of this species are narrow polyleges of certain Leguminosae, Zygophyllaceae, and Solanaceae but both sexes visit a variety of plants for nectar. Hurd and Linsley (1976:9) have recorded the male at flowers of *Helianthus annuus*, but this is no doubt a rare occurrence and an unimportant factor in the pollination ecology of this plant.

Family ANDRENIDAE

This is the largest family of bees in North America, containing over 1200 species currently assigned to 15 genera (Hurd, 1979). Most of the species, however, belong to the genera *Andrena* and *Perdita*, each of which includes more than 500 species in America north of Mexico. No less than eight of the 15 genera contain species that are involved in the pollination of *Helianthus*, viz., *Andrena* (14), *Calliopsis* (5), *Metapsaenythia* (1), *Nomadopsis* (1), *Perdita* (23), *Protandrena* (2), *Pseudopanurgus* (2), and *Pterosarus* (16). A large percentage of these species are oligoleges of the Compositae either primarily or secondarily associated with *Helianthus*. Thus these species are considered by us as among the most important pollinators of sunflowers.

Genus *Andrena* Fabricius

Although species of six subgenera of this genus have been found at the flowers of *Helianthus*, most of the species (7) belong to the subgenus *Callan-*

drena whose species mostly obtain their pollen from the flowers of Compositae. Of these, four are primarily dependent upon the pollen of *Helianthus* while three additional ones are secondarily so dependent. Two species of the subgenus *Cnemidandrena* are oligoleges of Compositae, one (*A. peckhami*) being primarily associated with *Helianthus* and the other (*A. chromotricha*) is secondarily associated with *Helianthus*. *A. (Simandrena) pallidifovea* is similarly secondarily associated with *Helianthus*, while the remaining three species, *A. lawrencei*, *A. microchlora*, and *A. prunorum* each belonging to different subgenera (*Euandrena*, *Micrandrena*, and *Plastandrena*) are casual polyleges of *Helianthus*.

1. *Andrena (Callandrena) accepta* Viereck

FIGURE 2

This is an oligolege of Compositae, with a primary preference for *Helianthus*. Of 219 females

bearing flower records examined by LaBerge (1967), 218 were taken from members of this plant family and of these, 194 were from *Helianthus*, including *H. angustifolius*, *H. giganteus*, *H. maximiliani*, *H. petiolaris*, *H. salicifolius*, and *H. scaberrimus*. Robertson (1894, 1898) recorded *A. accepta* from five species of sunflower in Illinois, including *H. mollis*. Later (1929) he provided additional data, listing the female taking nectar from *H. annuus*, both sexes at *H. divaricatus* (the females frequent and taking pollen), the female taking pollen from *H. rigidus* and nectar from *H. strumosus*, and both sexes abundant at *H. tuberosus* (the females gathering pollen). Cockerell (1914b) reported this bee at *H. lenticularis* in New Mexico, Michener (1947) from *H. radula* in Mississippi, and Bohart et al. (1950) and Rozen (1973) from *H. annuus* in Utah and Arizona, respectively. The species is widespread and ranges from New Jersey south to South Carolina, west to Alberta, eastern Oregon, eastern California (Owens Valley), Ari-

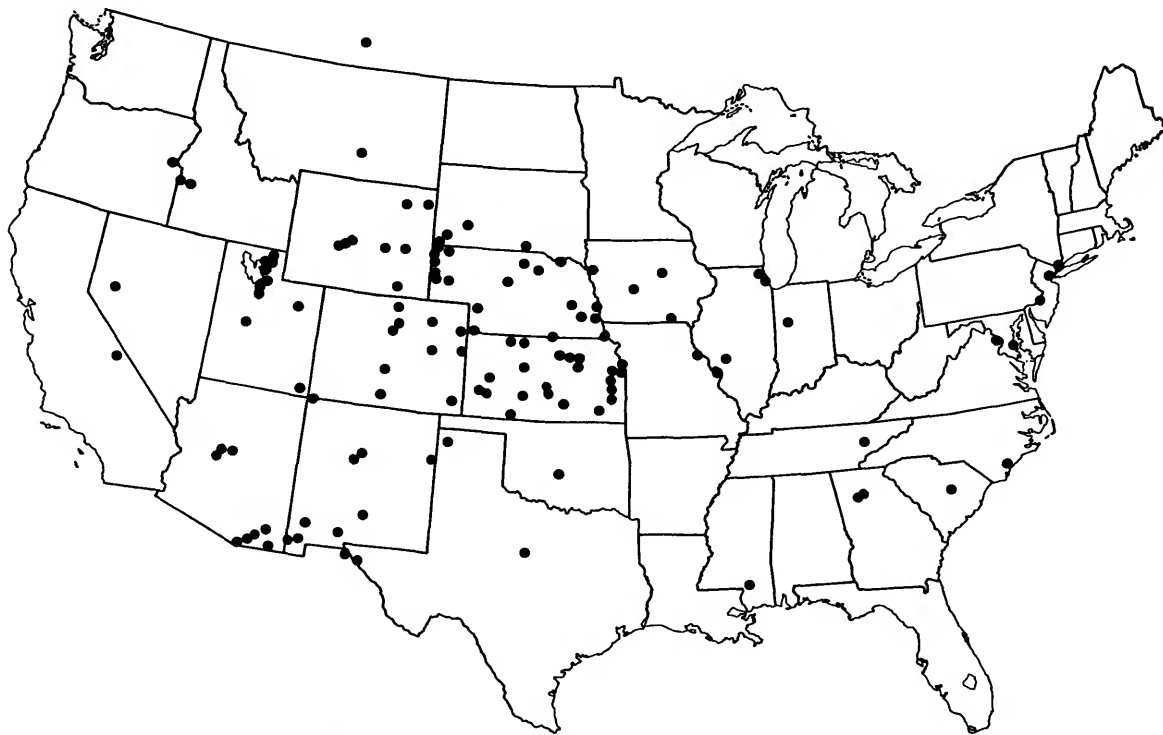


FIGURE 2.—Distribution of *Andrena (Callandrena) accepta* Viereck.

zona, and southward into Chihuahua, Mexico. It is absent from the Sonoran Desert. Graenicher (1909) did not find it on *Helianthus* in Wisconsin, nor did Stevens (1949a) in North Dakota.

For a discussion of the biology of *Andrena accepta*, see Rozen (1973). Details of collections of this species are presented in Tables A–E, G.

Additional records are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800–0859 1♀P, 1♀N (EGL, JML). SANTA CRUZ COUNTY: Sonoita 10 mi E, 7 Sep 77, *H. petiolaris*, 0830–0859, 1♀P (EGL, JML).

CALIFORNIA.—INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0800–0829, 3♀P (EGL, JML).

2. *Andrena (Callandrena) aliciae* Robertson

This species, an oligolege of the Compositae primarily associated with *Helianthus*, was reported (Robertson, 1894 and 1929) as taking pollen from *Helianthus tuberosus* in Illinois and from *H. strumosus* in Wisconsin (Graenicher, 1909) as well as nectar from *H. giganteus*. LaBerge (1967) included *Helianthus* sp., *H. angustifolius*, *H. divaricatus*, *H. giganteus*, *H. microcephalus*, *H. strumosus*, and *H. tuberosus* among his flower records for *A. aliciae*. Of 53 specimens bearing floral data examined by him, 28, representing eight collections, were from *Helianthus*. The range extends from New York south to Georgia and west to Minnesota, Nebraska, and Kansas.

3. *Andrena (Callandrena) duplicata* Mitchell

LaBerge (1967) recorded this species from *Helianthus* sp., *H. divaricatus*, *H. grosseserratus*, *Bidens coronata*, and *Solidago* sp. He lists it from New Jersey, North Carolina, Ohio, Illinois and Missouri. It is apparently an oligolege of the Compositae, secondarily associated with *Helianthus*.

4. *Andrena (Callandrena) haynesi* Viereck and Cockerell

Viereck and Cockerell (1914) described this species from a female taken on *Helianthus* sp. in War Bonnet Canyon, Sioux County, Nebraska, in June (J. C. Crawford, collector), and subse-

quently, Cockerell (1923) recorded a female from *H. petiolaris* at Xenia, Colorado. LaBerge (1967), regards it as an oligolege of *Helianthus* and reports that of 43 collections (74 females and 61 males) with floral data, 42 (72 females and 52 males) were from some species of this genus, mostly *H. petiolaris*. *Andrena haynesi* ranges from Alberta and North Dakota, south through Wyoming and Colorado to Texas. It flies primarily in July and August.

5. *Andrena (Callandrena) helianthi* Robertson

This species is an oligolege of the Compositae primarily associated with *Helianthus*. It was recorded taking nectar and pollen from *Helianthus grosseserratus* in Illinois by Robertson (1894), who later (Robertson, 1922, 1929) listed it among the most regular visitors to sunflowers in Carlinville, Illinois, where he had found it at five of the "eight" local species of *Helianthus*, including males taking nectar from *H. annuus* and *H. divaricatus*, both sexes numerous at *H. grosseserratus* and *H. rigidus* (the females taking pollen from each), and the female taking nectar from *H. tuberosus*. In Wisconsin, Graenicher (1909) reported females gathering pollen from both *H. giganteus* and *H. strumosus*.

Cockerell (1898a,b, 1911, 1914b) recorded females at *H. lenticularis* in Sterling and Boulder, Colorado, *H. annuus* in Albuquerque, New Mexico, and *H. annuus coronatus* at Goodville, Colorado. He regarded it as the most important sunflower bee in Colorado and Stevens (1949a) stated that it was a common sunflower bee all over the state of North Dakota, reporting only single specimens from *Grindelia* and two species of *Solidago*. LaBerge (1967) provided a summary of floral records from specimens examined by him. These included 234 females and 130 males, of which 215 and 119, respectively, were from some species of *Helianthus*. He listed *H. sp.*, *H. annuus*, *H. coloradensis*, *H. coronatus*, *H. divaricatus*, *H. giganteus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. rigidus*, *H. subrhomboides*, and *H. tuberosus* as flower hosts. In California, Moldenke and Neff (1974) recorded two males and four females from *H. annuus* in

Siskiyou County, California.

A collection record of this species at a major sampling site is presented in Table A. A previously unpublished record is as follows:

ARIZONA.—APACHE COUNTY: Nutrioso 8 mi N, 16 Aug 64, *H. annuus*, 1♂ (C. D. Michener, collector; specimen at University of Kansas, Lawrence.)

6. *Andrena (Callandrena) pecosana* Cockerell

LaBerge (1967) lists *Helianthus* among the few known flower hosts for this species, all Compositae (*Grindelia*, *Gutierrezia sarothrae*, *Heliopsis*, and *Viguiera annua*). It occurs from Colorado and Utah to Arizona, New Mexico and south into Mexico (Chihuahua, Hidalgo, Jalisco, and Zacatecas). Collection records for this species at flowers of *H. petiolaris* may be found in Table A. It is evidently an oligolege of the Compositae secondarily associated with *Helianthus*.

7. *Andrena (Callandrena) simplex* Smith

This species is an oligolege of Compositae secondarily associated with *Helianthus*, preferring *Solidago* and *Aster* (LaBerge, 1967), but it has been taken on *Helianthus tuberosus*. It ranges from New Hampshire to North Carolina, west to Minnesota, Nebraska, and Kansas.

8. *Andrena (Cnemidandrena) chromotricha* Cockerell

This species, more commonly known as *A. clypeonitens* Cockerell, was recorded by Graenicher (1909) taking pollen from *H. giganteus* and *H. strumosus* in Wisconsin. Stevens (1949a), under the names *A. clypeonitens* and *A. integra* Smith, recorded females of what is presumed to be this species at the flowers of *H. annuus*, *H. rigidus*, and *H. tuberosus* and both sexes at *H. maximiliani* in North Dakota. Mitchell (1960) reported a female of *A. recta* Mitchell (declared a synonym of *A. chromotricha* herein, page 00) on *H. annuus* at Crookston, Minnesota, in July. Donovan (1977) reported females taking pollen and nectar from *H. sp.*, *H. maximiliani*, and *H. tuberosus*. *Andrena*

chromotricha has been recorded from southern Canada (Ontario and Manitoba) south into New York, Ohio, Iowa, and Nebraska and west to Colorado, Utah, and Arizona. It appears to be an oligolege of the Compositae, but only secondarily associated with *Helianthus*.

9. *Andrena (Cnemidandrena) peckhami* Cockerell

Andrena peckhami was stated by Graenicher (1910b) to be oligolectic on Compositae, mostly sunflowers, in Wisconsin. Mitchell (1960) recorded *Baptisia* and *Solidago* as floral hosts, and Donovan (1977) listed pollen and nectar records from *Cirsium arvense* and *Sonchus arvensis*. The species ranges from southern Canada (Manitoba and Ontario) south to North Carolina and is an oligolege of the Compositae primarily associated with *Helianthus*.

10. *Andrena (Euandrena) lawrencei* Viereck and Cockerell

This is apparently a polylectic bee ranging from British Columbia to northern California, Utah, and Nebraska. Moldenke and Neff (1974) listed five females from *Helianthus nuttallii* in Eldorado County, California. LaBerge and Ribble (1975) also included *Helianthus nuttallii* among their flower records. It is apparently a casual polylege of *Helianthus*.

11. *Andrena (Leucandrena) recta* Mitchell

Mitchell (1960) reported a female of this species on *Helianthus annuus* at Crookston, Minnesota, in July. Since the completion of this study, one of us (LaBerge) has examined the holotype and finds that this is a synonym of *Andrena (Cnemidandrena) chromotricha* Cockerell (new synonymy).

12. *Andrena (Micrandrena) microchlora* Cockerell

Helianthus is included by Ribble (1968) among 17 genera of plants recorded on specimens of this

species examined by him. The species is primarily confined to western North America and appears to be a casual polylege of *Helianthus*.

**13. *Andrena (Plastandrena) prunorum*
Cockerell**

This is a polylectic species visiting a wide variety of plants for pollen and/or nectar. LaBerge (1969) listed 77 genera containing host plants, including *Helianthus*. It is primarily a western North American species, the nominate form ranging from southern British Columbia east to southern Saskatchewan and western North Dakota and south to Texas and Baja California; the subspecies *A. p. sinaloa* from Sinaloa and Baja California to southern Arizona. It is not regarded as an important pollinator of sunflowers since it appears to be only a casual polylege.

**14. *Andrena (Simandrena) pallidifovea*
(Viereck)**

Andrena pallidifovea is a common Pacific Coast species ranging from Washington to Utah and southern California. According to Timberlake (1951) it is a late vernal species that collects pollen from Compositae, including *Helianthus gracilentus* in southern California. It thus appears to be an oligolege of the Compositae secondarily associated with *Helianthus*.

Genus *Protandrena* Cockerell

This is a North American genus of panurgine bees whose species were recently revised by Timberlake (1976). Only the two species discussed below have been taken at the flowers of *Helianthus*.

15. *Protandrena bancrofti* Dunning

Timberlake (1976) has reported a number of genera containing floral hosts for this polylectic species, including *Helianthus*. It ranges from Wy-

oming, North Dakota, and Illinois to Arizona, New Mexico, and Texas and south into central Mexico. It is apparently a casual polylege of *Helianthus*.

16. *Protandrena mexicanorum* (Cockerell)

Females have been recorded from flowers of *Kallstroemia grandiflora* and *Solanum rostratum* and males from *Asclepias* (Timberlake, 1955). Insofar as is known, this species visits the flowers of *Helianthus* for nectar only (Table D).

Genus *Pseudopanurgus* Cockerell

Two of the 12 species of this genus, which is found only in North America, are oligoleges of the Compositae primarily associated with *Helianthus*. Insofar as is known, the species of this genus, recently revised by Timberlake (1973), all visit flowers of the Compositae and it therefore seems likely that some additional species will be found to visit sunflowers.

17. *Pseudopanurgus aethiops* (Cresson)

FIGURE 3

This is the largest species of the genus and is common from Nebraska, Kansas, and Texas west to Utah and southeastern Arizona (Timberlake, 1973). The species is restricted to Compositae and is primarily found on *Helianthus*, but also collects pollen from *Baileya*, *Encelia*, *Grindelia*, *Heterotheca*, *Melampodium*, *Prionopsis*, and *Verbesina*. Cockerell (1898b) recorded it from *Helianthus annuus* at Albuquerque, New Mexico, and from *Helianthus* sp. in Mesilla Valley, New Mexico (Cockerell, 1898a, 1906b).

Collection records of *P. aethiops* at major sampling sites may be found in Tables A-E. Addi-

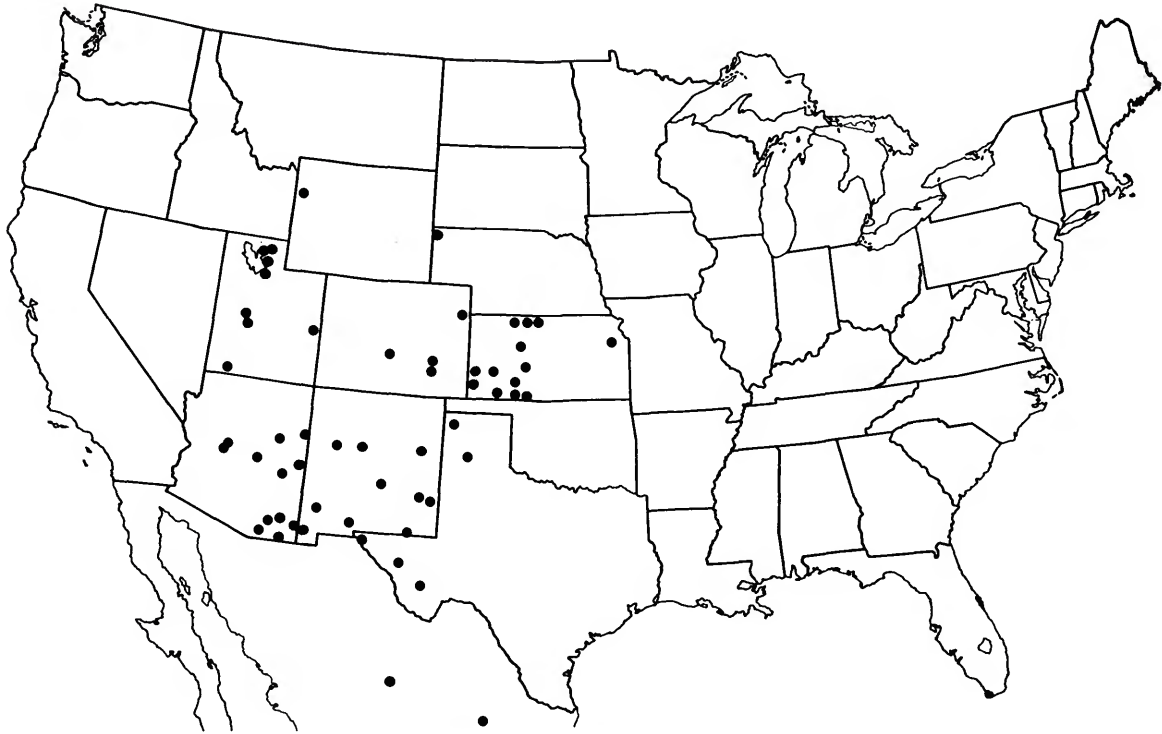


FIGURE 3.—Distribution of *Pseudopanurgus aethiops* (Cresson).

tional data are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0830–0859, 1♀P (EGL, JML); Sonoita, 16 Aug 74, *H. annuus*, 0800–0829, 1♀P (EGL, JML); Sonoita 10 mi E, 7 Sep 77, *H. petiolaris*, 0830–0859, 1♀P (EGL, JML).

18. *Pseudopanurgus rugosus* Robertson

This species, which occurs from Maryland to Georgia and west to Illinois, Nebraska, Kansas, and Texas, is an oligolege of the Compositae primarily associated with *Helianthus*. It has been recorded taking pollen from flowers of *Helianthus divaricatus* and *H. tuberosus*, and nectar from *H. mollis* in Illinois by Robertson (1929), from *H. radula* in Mississippi by Michener (1947), and from *H. annuus* and *H. petiolaris* in Kansas by Timberlake (1973), who listed *Heterotheca subaxillaris* as "*Helianthus subaxillaris*." Timberlake also provided *Helianthus* records from Georgia and

Nebraska. In addition, Robertson (1929) reported the species at *Heliopsis*, *Rudbeckia*, and *Silphium* and in Kansas both sexes have also been taken at the flowers of *Silphium speciosum* (Timberlake, 1973).

Genus *Pterosarus* Timberlake

More than 40 species of this genus are known from North America and based upon current information all of the species are presumed to be oligoleges of the Compositae. Of those species associated with *Helianthus*, four are primarily attached, nine are secondarily so, and two are known only from males, thus making it impossible to assess the intrafloral relationships of these species. Almost certainly as additional field investigations are undertaken other species of this genus will be discovered at sunflowers.

It seems worthwhile to mention that Grae-

nicher (1909, 1910b, 1935) did not find any species of this genus in his surveys of bees visiting *Helianthus* in Wisconsin.

19. *Pterosarus albitarsis* (Cresson)

In Illinois, females of this species were taken at flowers of *Helianthus* by Pearson (1933) and both sexes were reported by Robertson (1929) at *H. divaricatus* and *H. mollis* (the females collecting pollen). It ranges from Connecticut to Georgia and west to Illinois, Colorado, New Mexico, and Texas. In addition to the floral information presented above, the species also visits flowers of *Aster ericoides villosus*, *Brauneria pallida*, *B. purpurea*, *Coeopsis palmata*, *Lepachys pinnata*, *Rudbeckia hirta*, *R. laciniata*, *R. subtomentosa*, *Verbesina helianthoides* (Robertson, 1929) and is thus apparently an oligolege of Compositae secondarily associated with *Helianthus*.

20. *Pterosarus expallidus* (Swenk and Cockerell)

This species was described by Swenk and Cockerell (1907b) from a male captured at *Helianthus*. The female remains unknown and thus we have only a nectar record for this species.

21. *Pterosarus helianthi* (Mitchell)

Mitchell (1960) described this species from a female captured on *Helianthus annuus* in Tippecanoe County, Indiana, in August. Subsequently the species has been collected at the flowers of *Helianthus petiolaris* in New Mexico (Table A) and at flowers of *H. annuus* in Arizona (Table E). It is evidently an oligolege of the Compositae primarily associated with *Helianthus*.

22. *Pterosarus innuptus* (Cockerell)

This species was reported from *Helianthus annuus* and *H. petiolaris* in Nebraska by Swenk and Cockerell (1907b), from *H. annuus* var. *coronatus* in Colorado by Cockerell (1914b), and from *H. annuus*, *H. maximiliani*, *H. petiolaris*, *H. rigidus*, *H.*

rydbergii, *H. strumosus*, and *H. tuberosus* in North Dakota by Stevens (1919, 1950), where he considered it the most common species in the genus. This species ranges from Alberta, North Dakota, and Nebraska to Colorado, New Mexico, and Arizona and is considered by us to be an oligolege of the Compositae primarily associated with *Helianthus*.

23. *Pterosarus labrosiformis labrosiformis* (Robertson)

Both sexes of this subspecies have been recorded from *Helianthus divaricatus* and *H. tuberosus* (the females taking pollen), and the female taking nectar from *H. strumosus*, as well as other Heliantheae (Robertson, 1929). It has been reported from Illinois, North Carolina, and Georgia (Mitchell, 1960) and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

24. *Pterosarus labrosus* (Robertson)

Both sexes were recorded by Robertson (1929) at *Helianthus divaricatus* and *H. tuberosus* in Illinois, the females taking pollen. He also reported the species at *Rudbeckia triloba*. Mitchell (1960) added *R. lanceolata* and *Heliopsis* to these records. The species occurs from New York to North Carolina and west to Minnesota and is evidently an oligolege of the Compositae secondarily associated with *Helianthus*.

25. *Pterosarus leucopterus* (Cockerell)

This species was described from six males collected at flowers of *Helianthus petiolaris* at Xenia, Colorado (Cockerell, 1923), and since the female remains unknown we are unable to assess its intrafloral relationships.

26. *Pterosarus occiduus* (Timberlake)

This species appears to be primarily associated with *Haplopappus* and *Heterotheca*, but a female has been recorded from *Helianthus* in Madera Canyon, Santa Rita Mountains, Arizona

(Timberlake, 1967). The species is known only from Arizona (Cochise and Pima counties) and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

27. *Pterosarus perlaevis* (Cockerell)

Recorded from flowers of *Helianthus annuus* at Las Cruces, New Mexico, by Cockerell (1898c), the species is known from Colorado, New Mexico, and Arizona. Pending further information on its floral relationships we have classed this species as a probable oligolege of the Compositae secondarily associated with *Helianthus*.

28. *Pterosarus piercei piercei* (Crawford)

This subspecies has been recorded from *Helianthus annuus* in Nebraska (Swenk and Cockerell, 1907b) and *H. annuus*, *H. maximiliani*, *H. petiolaris*, *H. scaberrimus*, *H. tuberosus*, *Grindelia*, and *Solidago* in North Dakota (Crawford, 1915, Stevens, 1919). It occurs from North Dakota and Nebraska to Colorado and New Mexico and is evidently an oligolege of the Compositae primarily associated with *Helianthus*.

29. *Pterosarus renimaculatus* (Cockerell)

Stevens (1919, 1950) recorded this species from flowers of *Helianthus petiolaris*, *H. maximiliani*, and other Compositae in North Dakota. It ranges from Wyoming, North Dakota, and Nebraska to Colorado, New Mexico, and Texas. From the published records it appears to be an oligolege of the Compositae secondarily associated with *Helianthus*.

30. *Pterosarus rudbeckiae* (Robertson)

Robertson (1929) included a male visiting *Helianthus divaricatus* among the flower records for this species, along with four species of *Rudbeckia* and *Bidens aristosa*. Mitchell (1960) has added *Aster* and *Solidago*. The species is known from Illinois and Wisconsin and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

31. *Pterosarus simulans* (Swenk and Cockerell)

Swenk and Cockerell (1907b) described this species from examples of both sexes taken at *Helianthus* sp. and *H. annuus* in Nebraska. Subsequently, Crawford (1915) and Stevens (1919) recorded it from cultivated *H. annuus*, *H. maximiliani*, *H. petiolaris*, and *Taraxacum* in North Dakota. Thus the species appears to be an oligolege of the Compositae primarily associated with *Helianthus*.

32. *Pterosarus solidaginis* (Robertson)

Robertson (1929) recorded both sexes of this species from *Helianthus grosseserratus* (the females taking pollen), as well as a male at *H. tuberosus*. He also listed as hosts, species of *Bidens*, *Boltonia*, *Rudbeckia*, and *Solidago*. It ranges from northeastern United States to Mississippi and Illinois and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

33. *Pterosarus stigmatis* (Swenk and Cockerell)

Both sexes were recorded from *Helianthus* in Nebraska by Swenk and Cockerell (1907b) and subsequently reported by Cockerell (1923) at flowers of *H. annuus lenticularis* at Benkleman, Nebraska. The species visits other flowers of Compositae for nectar and pollen and is therefore apparently an oligolege of these plants with a secondary association with *Helianthus*.

Genus *Metapsaenythia* Timberlake

Included in this genus is a single species, *Metapsaenythia abdominalis* (Cresson), whose females collect pollen from flowers of *Monarda* (Labiatae), but visit these and a variety of other flowers, including *Helianthus* for nectar. The taxonomic relationships of this genus have been discussed by Timberlake (1973).

34. *Metapsaenythia abdominalis abdominalis* (Cresson)

This subspecies is common in Kansas and Texas. Females take pollen from *Monarda*, but

specimens have also been recorded at other flowers, including *Helianthus* (Timberlake, 1969a).

Genus *Nomadopsis* Ashmead

Of the 39 currently recognized species of this North American genus, only a single female of one species has been found at the flowers of *Helianthus*. The species of this genus seem sufficiently well known (Rozen, 1958, 1959, 1963, 1967) that it seems unlikely that any will be found to depend on the pollen of these flowers.

35. *Nomadopsis (Micronomadopsis) helianthi* (Swenk and Cockerell)

A female of this species was collected on *Helianthus* in Nebraska (Swenk and Cockerell, 1907b) and it has also been taken on *Helianthus* in south-eastern Arizona (Rozen, 1973). *Nomadopsis helianthi* occurs from Nebraska and New Mexico west to California and Mexico (Baja California) and appears to visit *Helianthus* and a variety of other flowers for nectar. The females are known to collect pollen from the flowers of *Euphorbia*, including *E. albomarginata* and *E. polycarpa* (Rozen, 1958), which appears to be its only pollen source. Since the completion of this study, Dr. J. G. Rozen, Jr. (pers. comm.) has informed us that he has observed this species collecting pollen from *Lepidium* in Arizona and New Mexico.

Genus *Calliopsis* Smith

This is a New World genus that occurs from southern Canada to Panama. All four subgenera recognized by Shinn (1967) are represented in America north of Mexico where 28 species have thus far been discovered. Of these, only the subgenera *Calliopsis* (1 species) and *Calliopsima* (4 species) have been found at sunflowers. The single species of the subgenus *Calliopsis* (*C. andreniformis* Smith) appears to seek nectar from these flowers, while the four species of the subgenus *Calliopsima* are oligoleges of the Compositae secondarily associated with *Helianthus*.

36. *Calliopsis (Calliopsis) andreniformis* Smith

A nectar-seeking female of this bee was taken on *Helianthus strumosus* in Wisconsin by Graenicher (1909). This is a polylectic species whose known sources of pollen include the flowers of *Aster ericoides villosus*, *Convolvulus*, *Desmodium marilandicum*, *D. paniculatum*, *Erigeron canadensis*, *Gerardia tenuifolia*, *Hedyotis purpurea*, *Lippia lanceolata*, *Lycopus sinuatus*, *Lythrum alatum*, *Malva neglecta*, *M. rotundifolia*, *Melilotus alba*, *M. officinalis*, *Oxalis stricta*, *Polygala sanguinea*, *Polygonum buxiforme*, *Psoralea onybrichis*, *Pycnanthemum pilosum*, *Trifolium pratense*, *T. procumbens*, *T. repens*, *Verbena bracteata*, *V. hastata*, *V. utricifolia*, and *Verbesina helianthoides*, but the species visits these and a wide variety of other flowers for nectar (Shinn, 1967). Recently, at 66 localities east of the Rocky Mountains, Dyer and Shinn (1978) have made a study of the floral taxa from which the females collect pollen to provision their nests. *Calliopsis andreniformis* ranges from south-eastern Canada (including the Maritime Provinces) south to Florida and west to Montana, Utah, Oklahoma, and eastern Texas.

37. *Calliopsis (Calliopsima) crypta* Shinn

Calliopsis crypta is known from the Chiricahua Mountains of southern Arizona and Chihuahua, Mexico. Shinn (1965) states that it collects pollen from *Heterotheca subaxillaris*, but notes that it also visits flowers of *Cirsium* and *Helianthus*. It is apparently an oligolege of Compositae secondarily associated with *Helianthus*.

38. *Calliopsis (Calliopsima) pectidis* Shinn

This species is primarily associated with Compositae in the southwestern United States and northwestern Mexico. It ranges through the deserts from western New Mexico to southern California and Baja California Sur. *Helianthus* is included among the flower records listed by Shinn (1965) and the species appears to be an oligolege of Compositae secondarily associated with this plant.

39. *Calliopsis (Calliopsima) pugionis* Cockerell

This southern Californian species is partial to Compositae (Shinn, 1967). A male has been recorded from *Helianthus gracilentus* in Riverside County by Moldenke and Neff (1974). Apparently *C. pugionis* is an oligolege of the Compositae and may be secondarily associated with *Helianthus*.

40. *Calliopsis (Calliopsima) rozeni* Shinn

Calliopsis rozeni occurs from western Texas to southeastern Arizona and south into Chihuahua and Coahuila, Mexico. Although it collects pollen primarily from *Heterotheca subaxillaris*, *Helianthus* is listed among the flower records provided by Shinn (1967). It is evidently an oligolege of Compositae and may be secondarily associated with *Helianthus*.

We have taken this species at sunflower as follows:

ARIZONA.—GRAHAM COUNTY: Franklin, 6 Jul 75, *H. annuus*, 1130–1159, 1♂ (EGL, JML).

Genus *Perdita* Smith

This is a very large genus of North American bees that has established through its component species a predominantly oligolectic relationship with the flora. Even though the genus occurs transcontinentally in southern Canada, the United States, and Mexico to as far south as Central America (Guatemala), it is centered in the more arid areas of northern Mexico and the adjacent southwestern United States. To date 23 species of *Perdita* belonging to five subgenera are now associated with *Helianthus*. Excluding *P. zebrata*, which apparently visits sunflowers only for nectar, there are 21 species of *Perdita* that are oligoleges of the Compositae either primarily associated with *Helianthus* (7 species) or secondarily so (14 species). In addition, one species (*P. gerhardi dallasiana* Cockerell) is apparently a casual polyge of *Helianthus*. In terms of subgenera, most species of *Perdita* visiting *Helianthus* (11) belong to the nominate subgenus and all of these are mem-

bers of the *octomaculata* species group. Membership in the other subgenera of *Perdita* includes *Cockerellia* (6 species), *Hexaperdita* (4 species) and *Pygoperdita* (1 species).

It is to be anticipated that as field studies progress, additional species of *Perdita* will be found to be involved in the intrafloral ecology of *Helianthus*.

41. *Perdita (Cockerellia) albipennis* Cresson

FIGURE 4

This is an extremely variable species with several currently recognized synonyms, most commonly used of which has been *P. lactipennis* Viereck and Cockerell. *Perdita albipennis* is an oligolege of the Compositae primarily associated with *Helianthus*. Four subspecies are presently recognized (Hurd, 1979).

Perdita (C.) albipennis albipennis ranges from Idaho and Wyoming to Wisconsin and southward to Texas, New Mexico, Arizona, and Sonora. It has been recorded from *Helianthus* sp. in New Mexico (Cockerell, 1898a), from *H. annuus* in Nebraska (Swenk and Cockerell, 1907a), Colorado (Cockerell, 1922; Timberlake 1953), and North Dakota (Timberlake, 1968). Timberlake (1953) also has reported both sexes as very abundant at *H. petiolaris* in western Kansas, Graenicher (1910a) at *H. occidentalis* in Wisconsin, and Cockerell (1911) at *H. lenticularis* in Colorado. New data are presented in Table D.

Perdita (C.) a. canadensis Crawford, which occurs from Alberta and North Dakota to Idaho and Utah, has been recorded from *Helianthus annuus*, *H. petiolaris*, *H. rigidus*, and *H. scaberrimus* in North Dakota (Stevens, 1919, 1950) and *H. petiolaris* in Colorado (Cockerell, 1936).

Perdita (C.) a. heliophila Cockerell, which ranges from Utah, Colorado, and New Mexico to Chihuahua, was described originally from *Helianthus* at Mesilla, New Mexico, by Cockerell (1916b), who later recorded it from *Helianthus* at Mesa Verde National Park, Colorado. Timberlake (1964, 1968) has provided additional records from Utah (*H. annuus*) and New Mexico (*H. sp.*).

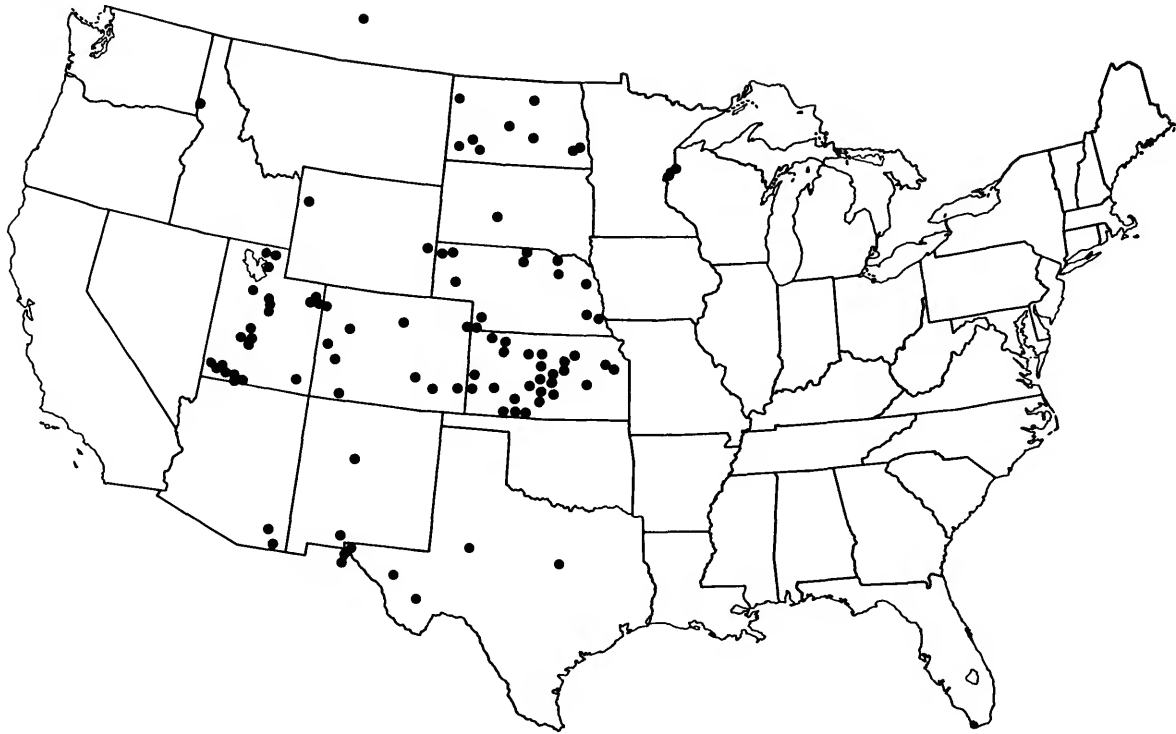


FIGURE 4.—Distribution of *Perdita (Cockerellia) albipennis* Cresson.

Perdita (C.) a. pallidipennis Graenicher occurs from eastern Kansas and Nebraska to Wisconsin and Indiana. The type series (Graenicher, 1910a) included specimens from various localities in Burnett County, Wisconsin, mostly taken at *Helianthus occidentalis* or *Rudbeckia hirta*. In 1914, Graenicher recorded *P. (C.) a. pallidipennis* from elsewhere in Wisconsin, including the dune region along Lake Michigan in southeastern Wisconsin and northeastern Illinois, gathering pollen from *H. occidentalis* and other sunflower-type Compositae, including *Rudbeckia hirta* and *Lepachys pinnata*. Timberlake (1953) recorded it from *Helianthus* in eastern Nebraska.

42. *Perdita (Cockerellia) bequaerti* Viereck

Two subspecies are recognized by Timberlake (1954), *P. (C.) bequaerti bequaerti* ranging from New Jersey to Florida, Mississippi and Minne-

sota, and *P. (C.) bequaerti indianensis* Cockerell occurring in Indiana, Oklahoma, and Tennessee. The first has been recorded from *Helianthus radula* in Mississippi by Michener (1947) and from *H. divaricatus* by Mitchell (1960). The species is an oligolege of the Compositae primarily associated with *Helianthus*.

43. *Perdita (Cockerellia) lingualis* Cockerell

Cockerell (1923) recorded this species from *Helianthus annuus lenticularis* at Oxford and Benkleman, Nebraska (as *P. albipennis*). It has also been reported at flowers of *Helianthus* in Utah and Kansas. The species ranges from Nebraska and Kansas to Utah, New Mexico, Texas, and Mexico (Tamaulipas). Collection records for this species may be found in Table C. It is apparently an oligolege of the Compositae primarily associated with *Helianthus*.

44. *Perdita (Cockerellia) scopata* Timberlake

This species occurs along the Gulf Coast of Texas where it has been taken at the flowers of *Coreopsis* and *Helianthus annuus* (Timberlake, 1953). It is closely related to *P. (C.) albipennis* Cresson (Timberlake, 1954) and like that species is an oligolege of the Compositae primarily associated with *Helianthus*.

45. *Perdita (Cockerellia) tricincta* Timberlake

This species, which may prove to be a geographic race of *P. albipennis* Cresson, is apparently an oligolege of the Compositae primarily associated with *Helianthus*. It occurs in southern Texas (Cameron, Hidalgo, and Starr counties) on *Helianthus annuus* (Timberlake, 1953).

46. *Perdita (Cockerellia) verbessinae* Cockerell

Although this species is primarily found at flowers of *Verbessina encelioides*, Cockerell (1896) also recorded a female and male at *Helianthus annuus* in New Mexico and a male at *Helianthus* sp. in Arizona (Tucson). The species ranges from Texas to Arizona and northern Mexico and is apparently an oligolege of Compositae secondarily associated with *Helianthus*. Collection records for males of this species at sunflower are given in Tables A, E.

47. *Perdita (Hexaperdita) alexi* Timberlake

Perdita alexi was described (Timberlake, 1968) from a female captured on *Heterotheca subaxillaris* at College Station, Brazos County, Texas, on 29 October. One additional specimen, a female paratype, was from near Aetna, Barber County, Kansas, on *Helianthus petiolaris* in July (LaBerge). On the basis of the known floral information, *P. alexi* is considered to be an oligolege of the Compositae secondarily associated with *Helianthus*.

48. *Perdita (Hexaperdita) ignota crawfordi* Cockerell

This subspecies is principally associated with *Grindelia squarrosa* but is also found on *Helianthus annuus* (Swenk and Cockerell, 1907a). It ranges from Nebraska to Oklahoma and Colorado. Like the other subspecies (*P. i. basalis* Timberlake, *P. i. ignota* Cockerell, *P. i. isopappi* Timberlake) this subspecies is an oligolege of the Compositae, but unlike those subspecies, which have not been taken at the flowers *Helianthus*, *P. i. crawfordi* has established a secondary association with sunflowers.

49. *Perdita (Hexaperdita) pratti* Cockerell

This species has been taken on *Helianthus petiolaris* and *H. cucumerifolius*, as well as *Heterotheca latifolia*, *H. subaxillaris*, and *Prionopsis petiolaris* (Timberlake, 1956). It is known to occur in Texas, Oklahoma, and Kansas and is regarded by us as an oligolege of the Compositae secondarily associated with sunflowers.

50. *Perdita (Hexaperdita) xanthisma* Cockerell

This species occurs from Wyoming to Nebraska and southward to Texas, New Mexico, and Arizona. It is apparently an oligolege of Compositae secondarily associated with *Helianthus*. Cockerell (1914b) reported it at *Helianthus* in Clarendon, Donley County, Texas, and Timberlake (1956, 1958) from *H. annuus* at Cullison, Pratt County, and Coldwater, Meade County, Kansas, and *H. petiolaris*, five miles north of Hutchison, Reno County, Kansas. Most recorded collection dates range between June and September.

51. *Perdita (Pentaperdita) nigroviridis* Timberlake

Timberlake (1968) reported the capture of five females on *Helianthus annuus* at San Antonio, Bexar County, Texas; previously he had reported this species from the flowers of *Gaillardia pulchella* and *Helenium* (Timberlake, 1958). It is apparently

an oligolege of the Compositae secondarily associated with *Helianthus*.

52. *Perdita (Perdita) affinis* Cresson

Males have been taken at flowers of *Helianthus petiolaris* and *Helianthus* sp. in Colorado (Timberlake, 1960). The habits of the female are not well known but it is presumably an oligolege of Compositae having been collected at the flowers of *Grindelia inornata*, *G. squarrosa*, *Haplopappus gracilis*, and *Solidago*. Its intrafloral relationship with *Helianthus* appears to be secondary. It has also been taken in New Mexico.

53. *Perdita (Perdita) aridella* Timberlake

Timberlake (1960) has recorded nine females and two males from *Helianthus* sp. at Oak City, Millard County, Utah, in June, and a male from *H. petiolaris* at Jensen, Uinta County, Utah, also in June. The species has been collected at the flowers of *Gutierrezia sarothrae*. It also occurs in Navajo County, Arizona. Evidently *P. aridella* is an oligolege of the Compositae secondarily associated with *Helianthus*.

54. *Perdita (Perdita) bruneri* Cockerell

Recorded from *Helianthus petiolaris* and other Compositae in North Dakota by Stevens (1919). The species ranges from southern Canada (Manitoba and Alberta) to Texas and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

**55. *Perdita (Perdita) dolichocephala*
Swenk and Cockerell**

Males of this species were recorded from *Helianthus* at Neligh, Antelope County, Nebraska (as *Perdita nebraskensis*, misidentification), and both sexes from Niobarra, Knox County, Nebraska, at *H.* sp. (as *P. dolichocephala*) by Swenk and Cockerell (1907a). Timberlake (1960) provided additional records of females and/or males from *He-*

lianthus including *H. subrhomboideus* and *H. petiolaris* in Nebraska and Kansas. Females were also reported at flowers of *Heterotheca subaxillaris*. The species ranges from Nebraska to Kansas and Colorado and is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

56. *Perdita (Perdita) fallax* Cockerell

This species frequents *Helianthus*, especially *H. petiolaris* but also occurs on other composites, including *Verbesina*, *Baileya*, *Heterotheca*, and *Grindelia*. It ranges from Nebraska and Montana to Colorado, Texas, New Mexico, and Arizona (Timberlake, 1960). It is an oligolege of the Compositae secondarily associated with *Helianthus*.

**57. *Perdita (Perdita) gerhardi dallasiana*
Cockerell**

Females of this subspecies have been taken at flowers of *Helianthus annuus*, as well as those of *Monarda*, the more usual host. Published records (Timberlake, 1960) are all from Texas. The nominate subspecies from Wisconsin, Illinois, and Indiana has thus far only been taken from the flowers of *Monarda punctata*. *Perdita g. dallasiana* is judged to be a casual polylege of *Helianthus*.

**58. *Perdita (Perdita) laticincta*
Swenk and Cockerell**

This species ranges from North Dakota, Nebraska, and Wyoming to Kansas and New Mexico. The females visit *Helianthus*, especially *H. petiolaris* (Swenk and Cockerell, 1907a; Cockerell, 1923; Stevens, 1950), but some specimens have been taken at the flowers of *Amorpha canescens*, *Haplopappus ciliatus*, and *Melilotus*. It is an oligolege of the Compositae apparently primarily associated with *Helianthus*.

59. *Perdita (Perdita) prionopsidis* Timberlake

Females have been taken at flowers of *Helianthus petiolaris* in Kansas as well as at the flowers of *Boltonia asteroides*, *Haplopappus ciliatus*, and *Het-*

erothera subaxillaris (Timberlake, 1960). Evidently the species is an oligolege of the Compositae secondarily associated with *Helianthus*.

60. *Perdita (Perdita) swenki* Crawford

Recorded from *Helianthus maximiliani* in North Dakota by Stevens (1919), the species also occurs in Nebraska, North Dakota, Minnesota, Michigan, Wisconsin, Illinois, and New York (Long Island) and visits, in addition, the flowers of *Chrysopsis*, *Grindelia*, *Liatris*, *Solidago juncea*, and *S. rigida*. It is an oligolege of the Compositae secondarily associated with *Helianthus*.

61. *Perdita (Perdita) tridentata* Stevens

This species was described from males collected on *Helianthus petiolaris* and *H. scaberrimus* in North Dakota (Stevens, 1919) and has been recorded from *H. petiolaris* in Nebraska and Kansas by Timberlake (1960). It has also been found at the flowers of *Haplopappus* and thus appears to be an oligolege of Compositae primarily associated with *Helianthus*.

62. *Perdita (Perdita) zebrata zebrata* Cresson

Although *P. z. zebrata* has been recorded from *Helianthus petiolaris* in Nebraska by Swenk and Cockerell (1907a) and Timberlake (1958), Cockerell (1896) remarked that it visits only the flowers of *Cleome* and Stevens (1950) has found it only at the flowers of *Cleome serrulata* in North Dakota (Cannon Ball, Medora, and Minot) from 3 August to 20 August. Custer (1929a) has discussed its nesting habits and described the nest and the larva. Rozen (1967) has presented some aspects of its life history, figured the larva and nest architecture and has confirmed that *P. zebrata zebrata* provisions its cells with pollen from the flowers of *Cleome*. He also has established that *Neolarra pruinosa* Ashmead is cleptoparasitic in the nests that he studied in Arizona.

**63. *Perdita (Pygoperdita) nebrascensis*
Swenk and Cockerell**

The type of this species is a female from Neligh, Antelope County, Nebraska taken on *Helianthus*, (Swenk and Cockerell, 1907a). No other flower data are known to us and we tentatively conclude that this species is an oligolege of the Compositae secondarily associated with *Helianthus*.

Family HALICTIDAE

Sixty-five species of 11 genera of this family have been associated with the flowers of *Helianthus*. All except the cleptoparasitic species *Sphcodes dichrous* are pollen-collecting species, many of which, however, visit these flowers for nectar only. There are a few species that are oligoleges of the Compositae either primarily or secondarily associated with sunflower. The majority of the species are apparently casual polyleges of *Helianthus* that visit also a variety of other flowers for pollen, nectar, or both. There are a few regular polyleges that visit these flowers (e.g., *Agapostemon texana*, *Halictus ligatus*) and are, like the oligoleges of the Compositae associated with *Helianthus*, decidedly important pollinators of these plants.

While we expect that some additional species in certain genera of the Halictidae will be found to be involved in the intrafloral ecology of *Helianthus* (e.g., *Dialictus*), we believe that the chief role of this family in the pollination of sunflowers is as discussed on the following pages.

Genus *Dufourea* Lepeletier

More than 60 species of this chiefly Holarctic genus are present in North America and many of the species are apparently highly restricted in their intrafloral relationships and thus oligolecty is a relatively common phenomenon. Only one species, treated below, is known to visit the flowers of *Helianthus*. It is an oligolege of the Compositae and is primarily associated with sunflower.

1. *Dufourea (Halictoides) marginata* (Cresson)

Swenk (1907) reported what is currently regarded as *D. (H.) marginata marginata* as flying in great abundance at flowers of the various species of *Helianthus* throughout the state of Nebraska; Robertson (1898, 1922, 1929) recorded it as one of the most regular visitors to *Helianthus* at Carlinville, Illinois, including the species *H. divaricatus* (♂, ♀P), *H. rigidus* (♀P), and *H. tuberosus* (♀N); and Stevens (1919) identified it as a common bee in North Dakota, especially at sunflowers (*H. petiolaris*, *H. scaberrimus*, *H. tuberosus*). Graenicher (1910b) recorded it from *Helianthus* in Wisconsin, Pearson (1933) from the Chicago area, and Michener (1947) in Mississippi. Records from *H. annuus* have been provided by Cockerell (1914b) for Colorado and Bohart et al. (1950) for Utah. It occurs from Alberta, Minnesota, Wisconsin, and Illinois to Mississippi, Colorado, and Utah.

Under the names *Panurgus halictulus* Cresson and *Halictoides marginatus* Cresson (subsequently re-named *Dufourea (Halictoides) marginata halictella* Michener), Cockerell (1897b, 1898c) recorded it from *Helianthus* at Santa Fe, New Mexico, in August and from *H. annuus* at Las Cruces, New Mexico, in September in great numbers.

Dufourea marginata is an oligolege of the Compositae primarily associated with *Helianthus*. Collection records of this species in the principal sampling sites are presented in Tables A, E.

Genus *Nomia* Latreille

This is primarily an Old World genus of bees that is represented by only 19 species in the Western Hemisphere, none being known south of Mexico. Of these, 12 have been found to visit the flowers of *Helianthus* but half of these only for nectar. The remaining six species are mostly oligoleges of the Compositae either primarily (3 species) or secondarily (2 species) associated with *Helianthus*. One species (*Nomia nortoni*) appears to be a casual polylege of sunflowers.

2. *Nomia (Curvinomia) angustitibialis* Ribble

Nomia angustitibialis is a relatively little-known species ranging from southeastern Arizona to Guerrero, Mexico. Most published flower records involve the introduced *Melilotus alba*, a highly attractive nectar source for Aculeate Hymenoptera and other insects. It has also been recorded from flowers of *Baccharis glutinosa*, *Condalia lycioides*, and *Larrea tridentata*. We have found females taking nectar from sunflower and other plants, but have not encountered them gathering pollen.

Our collection records for *N. angustitibialis* are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Jul 75, *H. annuus*, 0830-0859, 1♀N (EGL, JML). PIMA COUNTY: Rillito 5 mi W, 30 Jul 75, *H. annuus*, 1345-1359, 1♀N (AEM, MMM).

3. *Nomia (Curvinomia) fedorensis* Cockerell

According to Ribble (1965) this species occurs from southwestern Kansas to Vera Cruz, New Mexico, but is primarily known from southern and central Texas. He includes a record of a male at *Helianthus* sp. in his relatively short list of flowers visited (Compositae and Leguminosae). The species appears to visit the flowers of *Helianthus* for nectar only.

4. *Nomia (Curvinomia) mesillensis* Cockerell

Ribble (1965), under the name *N. foxii* Dalla Torre, records two males from *Helianthus* (locality not given), among a wide variety of flower records.

We have taken a male at sunflower as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0800-0829, 1♂ (EGL, JML).

Apparently the species visits *Helianthus* for nectar only.

5. *Nomia (Acunomia) nortoni nortoni* Cresson

This is a polylege of a wide variety of plants. It has been recorded from *H. maximiliani* at Dallas,

Texas, by Cockerell (1914b), and from *Helianthus* sp. by Ribble (1965). This subspecies occurs from Pennsylvania south to Florida and west to Idaho, Colorado, New Mexico, and northern Mexico (Coahuila). It appears to be a casual polylege of *Helianthus*.

6. *Nomia (Acunomia) melanderi* Cockerell

This is a polylectic species important in the pollination of alfalfa grown for seed, ranging from Washington to Wyoming and southern California. Ribble (1965) recorded it from *Helianthus* and it appears that this species probably visits the flowers of *Helianthus* for nectar only.

7. *Nomia (Epinomia) micheneri* Cross

A male of this species was recorded by Cross (1958) from *Helianthus* in Durango, Mexico. He reports the species from the Mexican Plateau, southern Arizona, and Texas. Collection records for this species in western New Mexico appear in Table A. Additional material of this species has been collected by Dr. T. J. Zavortink in Arizona (10.4 mi E Nogales) at the flowers of *Haplopappus gracilis* (♂) and in New Mexico (1.4 mi SW Rodeo) at the flowers of *Heterotheca subaxillaris* (♀P). The species is evidently an oligolege of the Compositae and may be primarily associated with *Helianthus*.

8. *Nomia (Epinomia) nevadensis angelesia* Cockerell

This subspecies ranges along the Pacific Coast of North America from Oregon to Nevada, southern California, and Baja California Norte, Mexico. It is polylectic. A nectar gathering female has been collected by P. H. Timberlake from *Helianthus gracilentus* in southern California just west of Perris, Riverside County. A collection record from one of our principal survey sites is presented in Table F. Like the following subspecies, this bee apparently visits the flowers of *Helianthus* for nectar only.

9. *Nomia (Epinomia) nevadensis arizonensis* Cockerell

Cross (1958) recorded males of this bee from *Helianthus* and one or both sexes from a variety of plants, mostly Compositae, especially *Grindelia squarrosa*. It turned up only once in our samples as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0800-0859, 2♂, 1♀N (EGL, JML).

This subspecies apparently visits the flowers of *Helianthus* for nectar only. It occurs from Utah, Arizona, and southern California (Colorado Desert) south to Jalisco, Mexico.

10. *Nomia (Epinomia) triangulifera* Vachal

This species was reported many years ago at flowers of *Helianthus* in New Mexico (Cockerell, 1899b, 1906b, 1914b) and *H. annuus* in Nebraska (Swenk, 1907). Recently, Cross (1958) more specifically recorded males and females from *H. annuus*, and *H. lenticularis* and males from *H. maximiliani* and *H. petiolaris*. Cross and Bohart (1960), however, in reporting on the nesting habits and provisioning of this species in a wide variety of soils from sand to clay in Utah and Kansas, concluded that *H. annuus* was the preferred host, although a few females with pollen loads have been taken on *Bidens involucreta*, *Grindelia squarrosa*, *Helianthus lenticularis*, *Rudbeckia triloba*, and *Silphium perfoliatum*. Cockerell (1898c), under the synonymous name *N. persimilis*, stated that females of this species mimic *Andrena helianthi* to such a degree that when collecting them he did not distinguish the two species.

Nomia triangulifera is an oligolege of the Compositae primarily associated with *Helianthus*.

11. *Nomia (Dieunomia) apache* Cresson

Two females were recorded from *Helianthus* at Victoria, Texas, by Cockerell (1910). The species ranges from Nebraska to Colorado, New Mexico, and Texas and is possibly an oligolege of the

Compositae secondarily associated with *Helianthus*.

12. *Nomia (Dieunomia) bolliana* Cockerell

This species is known from New Mexico and Texas. A female of the nominate subspecies was recorded from *Helianthus* at Wichita Falls, Texas, and both sexes from *Rudbeckia amplexicaulis* at Denton, Texas, by Cockerell (1910). He recorded the subspecies *N. b. helenii* from near Tilden, Texas, taking pollen and nectar from both *Helianthus microcephalum* and *Polypteris texana* (Cockerell, 1936). In view of our knowledge of the other *Helianthus*-visiting species of *Nomia*, it appears best at this time to regard this species as an oligolege of the Compositae secondarily associated with *Helianthus*.

13. *Nomia (Dieunomia) heteropoda* (Say)

FIGURE 5; PLATE 1

This is typically a sunflower bee. It was first recorded from *Helianthus* at Victoria, Texas, by Cockerell (1910). It is primarily associated with *H. annuus*, but unpublished records indicate that it is also commonly taken on *H. petiolaris*. Michener (1947) also reported it at *H. radula* in Mississippi. It ranges from Maryland to Florida and west to Nebraska, Utah, Arizona, and southern California (see Figure 5). However, it occurs discontinuously throughout this range, even where *Helianthus* is abundant, because of a marked preference for sand or sandy soil for a nesting substrate. The species has frequently been taken in sand dunes (Blair, 1935, and unpublished data by Lutz, 1919, and others). Hicks records burrows

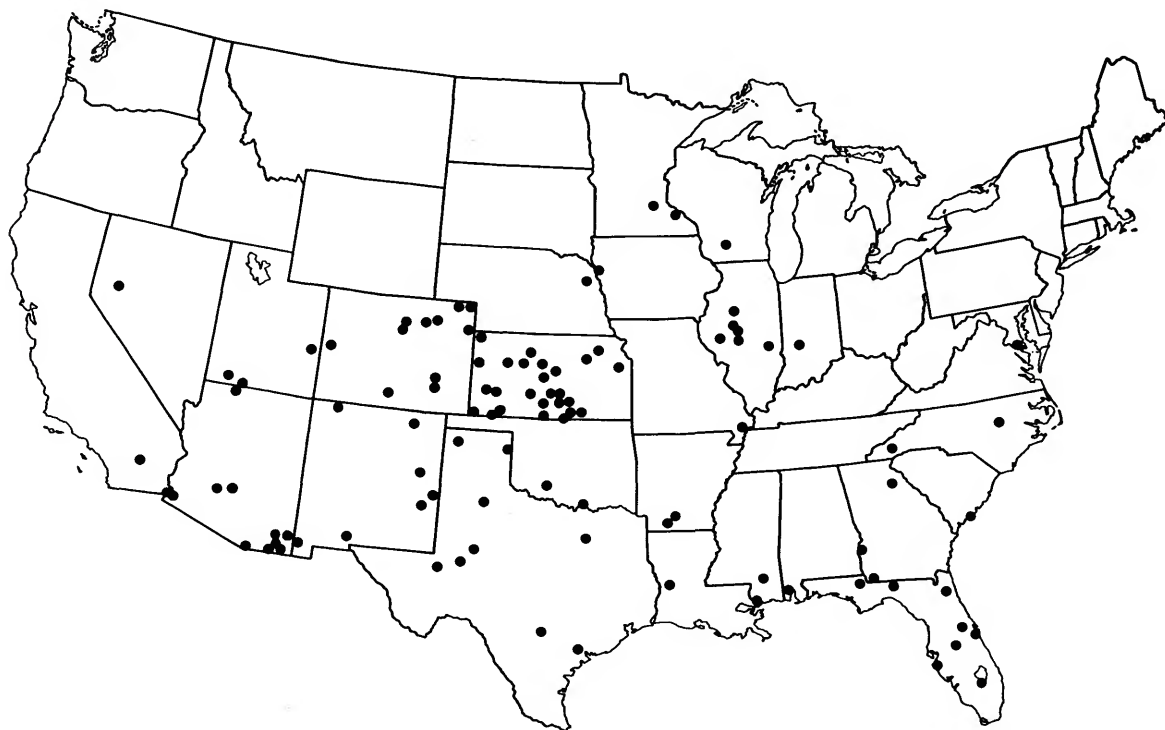


FIGURE 5.—Distribution of *Nomia (Dieunomia) heteropoda* Say.

extending vertically in the sand for three to four feet. In a more detailed account, Cross and Bohart (1960), describe and figure a burrow of this species where females were nesting in alluvial sand deposits at Lawrence, Kansas, along with those of *Nomia (Epinomia) triangulifera* with which they were collecting pollen from *Helianthus annuus*. The burrow excavated had a vertical shaft 94 cm deep, the last 14 cm of which was in a silt layer underlying the sand. The silt material was used to line the cells and the tunnel through the sand.

Perhaps because of the discontinuities in distribution that presumably have historically isolated some populations, numerous names have been applied to these as well as to individual variants, and the status of these remains to be determined (see comments by Mitchell, 1960).

Nomia heteropoda is a rapid pollen collector and is able to carry large amounts on the hind legs and to some extent on the abdomen. The males also become covered with pollen on the underside when visiting the flowers for nectar and may be seen periodically resting on the stems removing pollen with the legs. Mating takes place on the flowers and other males frequently attempt to dislodge the first male to achieve copulation. Most of the day they cruise the flowers like *Svastra* or *Melissodes*. When abundant, as at Indio, California, in September, the females can collect most of the pollen from a field of wild sunflowers between 0600 and 0900 hrs.

When a box of freshly pinned specimens was opened a strong lemony smell was evident. The collective odor in the box of dead specimens was definite but could not be identified with individual bees. Also, since both males and females were stored in the box it is not clear as to whether the odor is produced by one or both sexes.

The species is an oligolege of the Compositae primarily associated with *Helianthus*.

Details of collections of *N. heteropoda* in major sampling areas may be found in Tables B-D and F.

In addition, Dr. Thomas J. Zavortink has collected males of this species at 7 mi NNW Animas, Hidalgo County, New Mexico, on 30 August 1974

from the flowers of *H. annuus* between 1430 and 1500 MST.

Genus *Augochloropsis* Cockerell

This is a Western Hemisphere genus of bees that seems to be centered in the tropics but extends into the temperate regions of North and South America. Of the three species that occur in the United States two have been taken at the flowers of *Helianthus* with sufficient regularity to be considered casual polyleges of that plant.

14. *Augochloropsis (Paraugochloropsis) metallica metallica* (Fabricius)

Robertson (1929) reported both sexes of this species taking nectar from *H. annuus*, females taking nectar from *H. tuberosus* and pollen from *H. rigidus*, as well as both sexes at *H. divaricatus* and *H. grosseserratus*, from which the females were taking pollen. In Wisconsin, Graenicher (1909) found the bee collecting pollen from *H. strumosus*. The species and its subspecies are polylectic and widely distributed in eastern and southern United States to Panama but has been collected as far west as Arizona. It appears to be a casual polylege of *Helianthus*.

15. *Augochloropsis (Paraugochloropsis) sumptuosa* (Smith)

This species is reported by Mitchell (1960) from *Helianthus*, along with other flower records. The species ranges from Maine to Florida and west to South Dakota, Colorado, Arizona, and Texas. It is judged to be a casual polylege of *Helianthus*.

Genus *Augochlora* Smith

This is a large genus of chiefly tropical American bees some of whose species extend into the temperate regions of both North and South America. Of the five species present in America north of Mexico only the one discussed below has been found at the flowers of *Helianthus*.

16. *Augochlora (Augochlora) pura* (Say)

Mitchell (1960) recognizes two subspecies, the wide ranging nominate form occurring throughout most of North America east of the Dakotas and Texas, and *A. pura mosieri* Cockerell from southern Florida. He includes *Helianthus* among the many flower records for *A. p. pura* but not in his records for *A. p. mosieri*. Graenicher (1930) reported this species at *Helianthus debilis* in the Miami region of Florida (as "*A. festiva*"). Since he also included "*A. pura*" in his list of species, it is possible that his record from *Helianthus debilis* refers to the subspecies *mosieri*.

This species appears to be a casual polylege of *Helianthus*.

Genus *Augochlorella* Sandhouse

Bees of this genus are found only in the Western Hemisphere and are found on both the North and South American continents. Eight species are present in America north of Mexico and of these, six are known to visit the flowers of *Helianthus*. All are casual polyleges of that plant except *Augochlorella pomoniella*, which apparently visits the flowers for nectar only.

17. *Augochlorella aurata* (Smith)

This is a polylectic species ranging from eastern United States (North Carolina, Georgia, Florida, and Alabama) to Texas and northern Mexico. Robertson (1898, 1929) provides a long list of flower records from Illinois, including *Helianthus*, but his records attributed to this species are misidentifications since *A. aurata* is not known to occur in Illinois (Ordway, 1966a). Apparently this species is a casual polylege of *Helianthus*.

18. *Augochlorella bracteata* Ordway

This polylectic species was described from individuals taken on *Prosopis*, but Ordway (1966a) also includes *Helianthus* among her flower records. The range extends from eastern Texas to Hidalgo,

Mexico. It appears to be a casual polylege of *Helianthus*.

19. *Augochlorella gratiosa* (Smith)

Ordway (1966a) includes *Helianthus* among her flower records for this species, which ranges from Florida west to Texas. Presumably the species is a casual polylege of *Helianthus*.

20. *Augochlorella persimilis* (Viereck)

In Illinois, Robertson reported the females of *A. persimilis* taking pollen from *Helianthus mollis*. Although *A. persimilis* has been recorded from *Helianthus* in field studies by Ordway (1966a), she reports that females ignored sunflowers in the laboratory, even when they were producing an excess of pollen, apparently preferring other pollen sources (Ordway, 1966b). The species ranges over most of the eastern United States except northeast Florida and the coastal areas of the southeast and occurs as far west as Texas and Minnesota. It is evidently a casual polylege of *Helianthus*.

21. *Augochlorella pomoniella* (Cockerell)

Augochlorella pomoniella ranges from southwestern Utah, western Nevada, and central California southward to the Cape Region of Baja California and Costa Rica. The females are polylectic. Ordway (1966a) includes *Helianthus* among her flower records for the species. Apparently this species visits the flowers of *Helianthus* for nectar only:

Our single record from sunflower is the following:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0800-0829, 1♂ (EGL, JML).

22. *Augochlorella striata* (Provancher)

The female of this species was reported taking pollen from *Helianthus giganteus* and *H. strumosus* in Wisconsin by Graenicher (1909) and at *H. lenticularis* in Colorado by Cockerell (1911) (as

Augochlora coloradensis). Stevens (1921) found males at *H. maximiliani* and *H. tuberosus* in North Dakota. It ranges from Quebec to Florida and west to New Mexico and South Dakota.

Although Ordway (1966a) lists *Helianthus* among the flowers from which this species has been collected, in the laboratory she found that the females ignored sunflowers even when they produced so much pollen that it dropped off of the flower head (Ordway, 1966b), even though other composites were utilized as pollen sources.

The species is evidently a casual polylege of *Helianthus* that visits a great variety of other flowers for nectar and/or pollen (Hurd, 1979).

Genus *Agapostemon* Guerin-Meneville

This is a Western Hemisphere genus of bees that occurs on both the North and South American continents as well as the West Indies. Fourteen species are known to be present in America north of Mexico (Roberts, 1969, 1972a,b, 1973a), and many of these (9 species) have been taken at the flowers of *Helianthus*. Except *Agapostemon texana* Cresson, which is a regular polylege of sunflowers, the other eight species appear to be casual polyleges.

23. *Agapostemon angelicus* Cockerell

Agapostemon angelicus is a common polylectic species in the arid southwest and northern Mexico. It ranges from North Dakota, Colorado, and Iowa south to Texas, New Mexico, Arizona, southern California, and Mexico (Chihuahua, Durango and Sonora). Females gather pollen most actively early and late in the day. They have been reported at flowers of *Cucurbita*, *Mentzelia*, *Camissonia*, *Oenothera*, and *Larrea* (Hurd and Linsley, 1975), and by Moldenke and Neff (1974) from *Helianthus annuus* in Kern, Los Angeles, and Riverside counties, California, and *H. gracilentus* in Riverside, Los Angeles, and San Diego counties. The species is apparently a casual polylege of *Helianthus*.

Collections of *A. angelicus* are reported in Tables B-E. In addition we have taken an individual

from sunflower as follows:

ARIZONA.—SANTA CRUZ COUNTY: Sonoita, 16 Aug 74, *H. annuus*, 1♂ (PDH, AEM, MMM).

24. *Agapostemon cockerelli* Crawford

This polylectic species is particularly abundant in southeastern Arizona, southern New Mexico, western Texas, and the Mexican Plateau, but actually ranges northward through Colorado to Wyoming. Like other desert *Agapostemon*, females take pollen early and late in the day. They have been captured at flowers of *Cucurbita*, *Camissonia*, *Oenothera*, *Mentzelia*, and *Larrea* (Hurd and Linsley, 1975) but have not been reported previously from *Helianthus*. The species is apparently a casual polylege of this plant.

Collection records from sunflowers are reported in Tables D, E (mostly males). An additional record is as follows:

ARIZONA.—PIMA COUNTY: San Xavier, 19 Aug 74, *H. annuus*, 1200-1229, 1♂ (PDH, AEM, MMM).

25. *Agapostemon femoratus* Crawford

This is a widely distributed species ranging from British Columbia, Alberta, and North Dakota south to New Mexico, Arizona, Nevada, California, and Mexico (Baja California). Moldenke and Neff (1974) record three females and two males from *Helianthus gracilentus* in Riverside County, California. The species appears to be a casual polylege of *Helianthus*.

26. *Agapostemon melliventris* Cresson

Agapostemon melliventris is a widespread species in the western United States (Montana, Idaho, South Dakota, south to Texas, New Mexico, Arizona, and California) and northern Mexico. Females are polylectic and gather pollen in the early morning and late afternoon. They have been reported from flowers of *Cucurbita*, *Datura*, *Camissonia*, and *Larrea* (Hurd and Linsley, 1975) but not previously from *Helianthus*. Timberlake (pers. comm.) captured a female taking pollen from *Helianthus niveus*, 18 mi S of Indio, Riverside

County, California, in March. The species is apparently a casual polylege of *Helianthus*.

In addition to data on *A. melliventris* recorded in Table E, we have taken specimens at sunflower as follows:

CALIFORNIA.—INYO COUNTY: Big Pine, 28 Aug 77, *Helianthus annuus*, 0630-0729, 1♂, 1♀P (EGL, JML).

27. *Agapostemon sericeus* (Forster)

This is a polylectic species of eastern North America ranging from Ontario and Maine to Florida and westward to Manitoba, North Dakota, Nebraska, Kansas, Oklahoma, and Texas. Graenicher (1909) recorded a male at *Helianthus strumosus* in Wisconsin and Robertson (1929) includes *H. grosseserratus* (♂, ♀P) among his many flower records. It appears to be a casual polylege of *Helianthus*.

28. *Agapostemon splendens* (Lepeletier)

Graenicher (1930) recorded this widespread polylege from *Helianthus debilis* in Florida. This species ranges from Ontario and Maine west to Saskatchewan and south to Florida, Alabama, Mississippi, Louisiana, Texas, and New Mexico. It is evidently a casual polylege of *Helianthus*.

29. *Agapostemon texanus* Cresson

This is a widely distributed polylectic species that occurs transcontinentally from southern Canada and the United States to central Costa Rica. Cockerell (1923) collected a male from the flowers of *Helianthus lenticularis* at Oxford, Nebraska, and subsequently the species has been reported by Robertson (1929) taking pollen and nectar from *H. tuberosus* in Illinois. Females were collected from the flowers of cultivated *H. annuus* and from *H. petiolaris* and males from those of *H. maximiliani* in North Dakota (Stevens, 1921). Fischer (1950) recorded the species from *Helianthus* in Kansas but without stating the sex. Among the unpublished records in the P. H. Timberlake collection are a pollen-collecting female taken on *H. annuus* at 5.2 mi E of Sunset, Lincoln County,

New Mexico, and a nectar seeking female at 1.5 mi W of Perris, Riverside County, California on *H. gracilentus*.

On the basis of this information and the detailed records cited below we regard this species as a regular polylege of *Helianthus*.

Details of collections of this species at major sampling sites are presented in Tables F, H, K, and M. Additional records include the following:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0800-0829, 14♂, 12♀P, 4♀N (EGL, JML). PINAL COUNTY: Eloy, 26 Jun 74, *H. annuus*, 0630-0659, 1♂ (AEM, MMM).

CALIFORNIA.—FRESNO COUNTY: Parlier, 7 Sep 75, *H. annuus*, 1400-1429, 1♀P, 1♀N (EGL, JML, AEM, MMM). LOS ANGELES COUNTY: Pico Rivera, 4 Jun 75, *H. annuus*, 1630-1659, 1♂ (AEM, MMM), 11 Aug 75, *H. annuus*, 0830-0900, 3♂, 2♀P (AEM, MMM). ORANGE COUNTY: Newport Beach, 27 Aug 76, *H. annuus*, 1400-1429, 8♂ (AEM, MMM), 13 Sep 75, 1015-1029, 1♂ (AEM, MMM), 21 Sep 75, 1500-1514, 1♂ (AEM, MMM), 25 Sep 77, 0800-0830, 1♀P (AEM, MMM). TULARE COUNTY: Tulare, 6 Oct 75, *H. annuus* 1600-1629, 1♂ (EGL, JML, AEM, MMM).

TEXAS.—TRAVIS COUNTY: Austin, 18 Sep 78, *H. annuus*, 1700-1729, 3♂, 5♀P (PDH).

30. *Agapostemon tyleri* Cockerell

This species ranges from eastern Arizona and southern New Mexico to Tehuacan, Puebla, Mexico. It has been reported from flowers of *Larrea tridentata* (Hurd and Linsley, 1975) but we have not been able to find other published flower records. It is evidently a casual polylege of *Helianthus* (Table C).

In addition, specimens have been taken as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0829, 3♀P (EGL, JML). SANTA CRUZ COUNTY: Duquesne Road, 6.9 mi SE Highway 82, 29 Aug 1973, *H. annuus*, 1000-1030, 2♀P (T. J. Zavortink).

31. *Agapostemon virescens* (Fabricius)

This species was recorded from *Helianthus* in Kansas by Walker (1936). It occurs throughout the eastern and central United States and southern Canada to the Pacific Northwest. Like other *Aga-*

postemon it is polylectic and its relationship to *Helianthus* appears to be casual.

Genus *Halictus* Latreille

Five species of this chiefly Holarctic genus have been found to visit the flowers of *Helianthus*. Only one of these, *H. ligatus*, whose range extends considerably beyond that of *Helianthus* in North America, visits the flowers with sufficient regularity to be classed as a regular polylege. The other species are evidently less regular in their floral visitation and are considered by us to be casual polyleges of *Helianthus*. Nonetheless, the species of this genus discussed below are regarded as important pollinators of these plants.

32. *Halictus (Halictus) farinosus* Smith

This is a western American species occurring from Montana and Nebraska west to British Columbia and south to New Mexico, Arizona, and California. The females, as their congeners, are polylectic. Moldenke and Neff (1974) record 12 females and two males from San Diego County, California, on *Helianthus gracilentus*.

On the basis of our sampling program this species is considered by us to be a casual polylege of *Helianthus*.

During the surveys this species was taken on sunflowers only once:

CALIFORNIA.—SAN DIEGO COUNTY: Vicinity of Laguna Junction and Interstate Highway 8, 13 Jun 74, *H. gracilentus*, 1300–1415, 11♀P, 7♀N (AEM, MMM).

33. *Halictus (Halictus) ligatus* Say

This widespread highly polylectic bee (see Roberts, 1973b) has been recorded from *Helianthus* many times throughout the country. Robertson (1894, 1898, 1922, 1929) reported it as one of the most regular visitors to *Helianthus* at Carlinville, Illinois, where he found it taking pollen from six species: *H. annuus*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. rigidus*, and *H. tuberosus*. Cockerell recorded it from sunflower in Virginia (at *H. annuus coronatus*), in California and Colorado (*H.*

annuus lenticularis) and Texas (*H. maximiliani*) (Cockerell, 1911, 1914b, 1915b,c, 1916a, 1923). It has also been collected at *H. debilis* in Florida by Graenicher (1930); *H. radula* in Mississippi by Michener (1947); and *H. sp.* in North Dakota by Stevens (1951c) and in Ontario (Knerer and Atwood, 1962). The species ranges from southern Canada to the West Indies and northern South America (Colombia to Trinidad). For discussions of its habits, see Roberts (1973b), Michener and Bennett (1977), and Litte (1977). The species is a regular polylege of *Helianthus*.

Although we have found males present in small numbers throughout the principal blooming period of sunflower in the sites sampled, beginning in June, we found them most abundant at Corcoran, California, on 5 October 1975. Between 0700 and 1400 hrs, 184 males were taken, along with 54 females (of which 48 were taking pollen), the two sexes together representing 35.6 percent of the bees visiting the flower heads during that period.

H. ligatus was found on sunflowers at all primary sites but one (see Tables A-F, H-M for details). Additional records from secondary survey sites are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 0800-0859, 2♂, 5♀P, 14♀N (EGL, JML). GRAHAM COUNTY: Franklin, 6 Aug 75, *H. annuus*, 1130-1159, 1♀P (EGL, JML). MARICOPA COUNTY: Theba, 28 Jun 74, *H. annuus*, 1130-1159, 1♂, 1♀P, 1♀N (AEM, MMM). PIMA COUNTY: Rillito, 2 Aug 75, *H. annuus*, 0700-0729, 13♀P, 1♀N (AEM, MMM); San Xavier, 19 Aug 74, *H. annuus*, 1200-1259, 2♂, 2♀N (PDH, AEM, MMM). PINAL COUNTY: Eloy, 26 Jun 74, *H. annuus*, 0630-0659, 2♂, 2♀N (AEM, MMM), 30 Aug 75, *H. annuus*, 0815-0929; 2♂, 5♀P, 2♀N (AEM, MMM). YUMA COUNTY: Wellton, 5 Sep 74, *H. annuus*, 1100-1129, 1♀N (AEM, MMM).

CALIFORNIA.—CONTRA COSTA COUNTY: Byron 4 mi E, 21 Jul 77, *H. annuus*, 0800-0829, 2♀P (EGL, JML, AEM, MMM). FRESNO COUNTY: Highway 99, Visalia-Hanford Junction, 22 Aug 76, *H. annuus*, 0730-0829, 3♀P (AEM, MMM). IMPERIAL COUNTY: El Centro, 29 Jul 75, *H. annuus*, 1000-1014, 3♀P, 1♀N (AEM, MMM); Holtville 3 mi W, 29 Jul 75, *H. annuus*, 1100-1140, 1♀P (AEM, MMM). KERN COUNTY: Copus Road between Highways 5 and 99, 22 Aug 76, *H. annuus*, 1130-1159, 6♀P (AEM, MMM); Lost Hills 3 mi S, 29 Aug 76, *H. annuus*, 1100-1129, 1♀P (AEM, MMM). LOS ANGELES COUNTY: Pico Rivera, 11 Aug 75, *H. annuus*, 7♀P, 2♀N (AEM, MMM); Sunland, Tujunga Canyon, 14

May 75, *H. annuus*, 1230–1244, 1♀P (AEM, MMM). MERCED COUNTY: Gustine 10 mi S, 27 Sep 76, *H. annuus*, 2♀P (AEM, MMM). RIVERSIDE COUNTY: Blythe, 29 Jun 74, *H. annuus*, 0800–0829, 1♂, 9♀N (AEM, MMM); Coachella, 8 Jun 76, *H. annuus*, 0900–0929, 1♀P (EGL, JML); Indio, 8 Jun 76, *H. annuus*, 0700–0829, 8♀P, 1♀N (EGL, JML). SAN JOAQUIN COUNTY: Manteca 7.5 mi N, 21 Aug 77, *H. annuus*, 1100–1129, 1♂, 3♀P (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Patterson, 21 Aug 76, *H. annuus*, 1315, 1♀P (AEM, MMM), 27 Jul 77, *H. annuus*, 0930–0959, 6♀P (EGL, JML, AEM, MMM).

TEXAS.—TRAVIS COUNTY: Austin, 18 Sep 78, *H. annuus*, 0900–1700, 4♂, 21♀P, 5♀N (PDH).

34. *Halictus (Halictus) rubicundus* (Christ)

This is a Holarctic polylectic species, ranging in North America from Alaska and Canada south to California, Arizona, Texas, and Florida. Graenicher (1909) reported both sexes at *Helianthus strumosus* in Wisconsin, the females taking pollen. Stevens (1951c) has recorded the species from *H. maximiliani* in North Dakota and Moldenke and Neff (1974) have listed it from an unidentified *Helianthus* in Los Angeles County, California. It is judged to be a casual polylege of *Helianthus*.

35. *Halictus (Seladonia) confusus* Smith

Halictus confusus is a widely distributed, polylectic bee occurring from the Atlantic to the Pacific in southern Canada and the United States. Two subspecies are recognized, *H. confusus confusus*, which occurs from Alaska to Nova Scotia, south to Florida, west to North Dakota and Texas, and *H. confusus arapahonum* Cockerell, which occurs from North Dakota to New Mexico and west to British Columbia, Oregon, and California. The nominate subspecies has been taken on *Helianthus strumosus* (♂, ♀P) in Wisconsin (Graenicher, 1909) and *H. annuus* (11♀) and more frequently at *H. divaricatus* (♂, ♀P) in Illinois (Robertson, 1929). Roberts (1972b) reports the bee essential to the production of marigold seed and of considerable importance in the production of *Zinnia* seed in Oregon. The subspecies *H. c. arapahonum* occurred in two of our samples taking nectar as follows:

ARIZONA.—PIMA COUNTY: Rillito 6 mi W, 27 May 74,

H. annuus, 0830–0859, 1♀N (AEM, MMM); San Xavier, 19 Sep 74, *H. annuus*, 1230–1259, 1♀N (PDH, AEM, MMM).

It is apparently a casual polylege of *Helianthus*.

36. *Halictus (Seladonia) tripartitus* Cockerell

Halictus tripartitus is a species of western North America, ranging from Washington to California and Baja California, Mexico, and west to Idaho, Colorado, Arizona, New Mexico, and Texas. It is polylectic and among records of flowers visited in southern California, Moldenke and Neff (1974) include instances of a female and male at *Helianthus* sp. in Riverside and Fresno counties, respectively, and a female from *H. annuus* in Riverside County. The relationship of this species to *Helianthus* appears to be that of a casual polylege.

Genus *Lasioglossum* Curtis

Although this genus is represented in North America by 19 species including one Holarctic species, only the four species discussed below are known to visit the flowers of *Helianthus*. Except for *Lasioglossum mellipes* (only males of which have been taken at the flowers of *Helianthus gracilentus*), the species appear to be casual polyleges of *Helianthus*.

37. *Lasioglossum coriaceum* (Smith)

This is wide ranging species having been reported from Nova Scotia to Georgia and west to Alberta and New Mexico, extending southward in the Mississippi Valley to Illinois. It is a highly polylectic species obtaining pollen and nectar from a wide variety of plants. Robertson (1894, 1929) notes that it takes pollen and nectar from *Helianthus tuberosus* and Graenicher (1909) includes *H. strumosus* as a source of nectar and pollen in Wisconsin. It is regarded by us as a casual polylege of *Helianthus*.

38. *Lasioglossum mellipes* (Crawford)

As presently known, this is a species of southern California and Baja California Norte, Mexico. Males have been taken at flowers of *Helianthus*

gracilentus in San Diego County, California (Moldenke and Neff, 1974).

39. *Lasioglossum sisymbrii* Cockerell

Lasioglossum sisymbrii occurs widely in the west from British Columbia to Wyoming and New Mexico and south to Arizona and through California to Baja California, Mexico. It is polylectic and females have been reported at flowers of *Helianthus* sp. in Los Angeles County and *Helianthus niveus* in Riverside County, California, by Moldenke and Neff (1974). Hurd and Linsley (1975) reported females taking pollen from *Larrea tridentata*. In 1936, a female taking nectar from *H. annuus* was collected in Westwood Hills, Los Angeles County, California (EGL). It is evidently a casual polylege of *Helianthus*.

40. *Lasioglossum titusi* (Crawford)

This is a species of the west coast of North America, thus far known from Oregon and California. Among the flower records provided by Moldenke and Neff (1974) are 16 females from *Helianthus* sp. in Los Angeles County, California, and it appears that this species is a casual polylege of *Helianthus*.

Genus *Evylaeus* Robertson

Six species of this genus have been found visiting the flowers of *Helianthus*. Except *Evylaeus aberrans* (Crawford) whose females principally obtain their pollen from the flowers of *Oenothera*, the others are polylectic species that visit *Helianthus* for pollen and nectar (3 species) or for nectar only (3 species).

41. *Evylaeus aberrans* (Crawford)

This is a rather wide ranging species having been reported from North Dakota, Nebraska, Colorado, New Mexico, Oregon, California, and Canada (Alberta). The female collects pollen principally from flowers of *Oenothera* (Onagraceae), but also visits these and a wide variety of other plants

for nectar or occasionally pollen. The floral relationships and nesting biology of this species (as *E. galpinsiae*) have been discussed by Bohart and Youssef (1977b). Stevens (1921) has reported the capture of two females and nine males at the flowers of *Helianthus petiolaris* in North Dakota. Presumably they were seeking nectar.

42. *Evylaeus amicus* (Cockerell)

This polylectic southwestern species occurs from New Mexico to California. Described originally from females taken at *Sisymbrium* and plum in the Mesilla Valley, New Mexico (Cockerell, 1897b), we have taken it at a variety of desert plants in Arizona and California. For our only sunflower collection, a male, see Table E.

43. *Evylaeus argemonis* (Cockerell)

This species is not very well known in the literature. The female was described by Cockerell (1897a) from Paso de Telaya, Vera Cruz, Mexico, on flowers of *Argemone mexicana*, and *E. latifrons* (Viereck), regarded as a synonym, from Santa Clara County, California. Our only record from *Helianthus* is as follows:

CALIFORNIA.—LOS ANGELES COUNTY: PICO RIVERA, 15 May 75, *H. annuus*, 1♀N (AEM, MMM).

44. *Evylaeus kincaidii* (Cockerell)

Evylaeus kincaidii is a species of the Pacific Coast of North America, ranging from Washington to California. Among the flower records for this species in southern California provided by Moldenke and Neff (1974) are four females from *Helianthus* sp. in Los Angeles County. It appears to be a casual polylege of sunflower.

45. *Evylaeus pectinatus* (Robertson)

This is a polylectic species of eastern North America (Connecticut, New Jersey, Maryland, Illinois, and Missouri) that has been reported taking nectar from *Helianthus tuberosus* by Robertson (1929).

46. *Evylaeus pectoralis* (Smith)

This is also a polylectic species ranging from eastern Canada to Florida, west to Wisconsin, Nebraska, and Texas. Robertson (1894, 1898, 1929) includes *Helianthus* in his extensive list of flower records, the females taking pollen from *H. divaricatus*, *H. laetiflorus*, and *H. tuberosus*. Graenicher (1909) also reported it at *H. strumosus* (♂, ♀P) in Wisconsin. It is apparently a casual polylege of *Helianthus*.

47. *Evylaeus pectoraloides* (Cockerell)

This widespread polylectic species ranges from southwestern Canada to Colorado, New Mexico, Arizona, California, and northern Mexico. Cockerell (1897b) records a wide range of floral hosts in New Mexico. We have taken a single female from *Helianthus* (Table E). The species is evidently a casual polylege.

Genus *Dialictus* Robertson

Nearly 200 species of this very large genus are known to occur in America north of Mexico. Insofar as is known, all of the species are polylectic, although *Dialictus ornduffi* is reported (Hurd, 1970) to be narrowly polylectic obtaining all or most of its pollen from the flowers of *Jepsonia heterandra* (Saxifragaceae). Thus far 17 species of this genus have been found at the flowers of *Helianthus*. Of these 11 are casual polyleges of that plant and six apparently seek nectar only. At certain localities, *Dialictus pruinosiformis* has been found in relatively large numbers at sunflower (Table D). It is expected that many more species of this genus will be found to visit the flowers of *Helianthus* as field studies progress. We have records of two unidentified species (both males) taken at the flowers of *Helianthus annuus* at Benson, Arizona and Corcoran, California. These are in addition to the species discussed below.

48. *Dialictus albipennis* (Robertson)

Graenicher (1909) reported a male of this species at flowers of *H. strumosus* in Wisconsin. The

species is polylectic and ranges from Nova Scotia to Oregon and south to North Carolina, Illinois, and Colorado.

49. *Dialictus clematisellus* (Cockerell)

This species ranges in the southwest from New Mexico and Utah to California. Cockerell (1904) reported that it occurred in numbers at flowers of *Clematis ligusticifolia* at Pecos, New Mexico, but we know of no other published flower records. We have encountered females taking nectar from *H. annuus* (Table E).

50. *Dialictus illinoensis* (Robertson)

This eastern North American species (Nebraska and Minnesota to Nova Scotia and south to Texas and Georgia) is polylectic. Among the wide range of reported flowers visited, Robertson (1929) includes a male at *Helianthus divaricatus*.

51. *Dialictus imitatus* (Smith)

This is a highly polylectic bee that has been recorded taking pollen from *Helianthus annuus* and *H. tuberosus* at Carlinville, Illinois (Robertson, 1929, as *Chloralictus sparsus*). It ranges from Quebec and the New England states to Florida and west to Minnesota and California. It is apparently a casual polylege of *Helianthus*.

52. *Dialictus impavidus* (Sandhouse)

Thus far this species has been recorded from California, Arizona, and Nevada. Moldenke and Neff (1974) list a female at *Helianthus* in San Diego County in their treatment of bees of California. Since no additional records of this species are known to us from *Helianthus* we regard this species as a nectar visitor to that plant.

53. *Dialictus incompletus* (Crawford)

This is a common polylectic species of the southwestern United States, primarily found in the desert areas of New Mexico, Arizona, southern Nevada, and California. Moldenke and Neff

(1974) report the capture of three females at flowers of *Helianthus annuus* in Riverside County and one at *Helianthus* sp. in Los Angeles County, California. It is apparently a casual polylege of *Helianthus*. We have collected the following specimens:

CALIFORNIA.—CONTRA COSTA COUNTY: 4 mi E of Byron, 21 Jul 77, *H. annuus*, 0800-0829, 1♀P (EGL, JML, AEM, MMM). STANISLAUS COUNTY: 6.5 mi N of Grayson, on Kasson Road, 27 Jul 77, *H. annuus*, 1100-1129, 3♀N (EGL, JML, AEM, MMM).

54. *Dialictus marinus* (Crawford)

Recorded from *Helianthus debilis* in Florida by Graenicher (1927, 1930) and from *Alternanthera floridana*, *Bidens*, *Helianthus*, and *Parthenocissus* by Mitchell (1960), this species occurs along the Atlantic seaboard from Massachusetts to Florida and is considered by us to be a casual polylege of *Helianthus*. The type series was swept from grass (*Scirpus*, *Ammophila*, etc.) growing along the strand within the beach at Ocean City, New Jersey, and possibly the bees were flying up from their nests in the sand.

55. *Dialictus microlepoides* (Ellis)

This is a polylectic species occurring from New Mexico to California and northern Mexico. We have found it visiting sunflower but only for nectar. In addition to the data in Table E we record:

ARIZONA.—PIMA COUNTY: San Xavier, 19 Sep 74, *H. annuus*, 1230-1259, 1♀N (PDH, AEM, MMM).

56. *Dialictus nevadensis* (Crawford)

Cockerell (1916a) recorded this species from *Helianthus lenticularis* at Orange, California. Earlier he had noted that this species occurs at the flowers of a wide range of plants including the flowers of peach, almond, and apricot. The species, which occurs in the southwestern United States, is apparently a casual polylege of *Helianthus*.

57. *Dialictus oleosus* (Cockerell)

This is a southwestern species ranging from Colorado and New Mexico to Arizona. We have not encountered published flower records for either sex. Our sunflower collection is recorded in Table E; the species appears to visit *Helianthus* for nectar only.

58. *Dialictus pilosus pilosus* (Smith)

Dialictus pilosus, which is widely distributed from Colorado and Minnesota to southern Canada (Nova Scotia) and south to Georgia, is a highly polylectic species. It appears to be a casual polylege of *Helianthus* since the nominate subspecies was recorded by Robertson (1922, 1929) from five species of sunflower, one of which, *H. divaricatus*, it visited regularly.

59. *Dialictus pruinosiformis* (Crawford)

This is a common and widespread species in central and southwestern United States, ranging from Alberta, Canada, through South Dakota, Nebraska, and Iowa to Texas, New Mexico, Arizona, and California. The species is polylectic and is apparently a casual polylege of *Helianthus*, but not many of its host flowers have been reported in the literature. The female has been recorded from *Helianthus annuus lenticularis* (Cockerell, 1911) and *H. petiolaris* (Cockerell, 1923) in Colorado. Hurd and Linsley (1975), in their surveys of bee visitors to *Larrea tridentata*, found it the most abundant species of *Dialictus* at flowers of this plant, collecting 184 females and 181 males in May and June at sites ranging from western New Mexico to Tucson, Arizona. For details of collections for this species at sunflowers, see Tables C, D.

60. *Dialictus punctatoventris* (Crawford)

Known thus far only from southern California and Baja California Norte, Mexico, *D. punctatoventris* has been recorded from flowers of *Helianthus* based upon a female from San Diego County,

California (Moldenke and Neff, 1974). It is evidently a casual polylege of *Helianthus*.

61. *Dialictus tegulariformis* (Crawford)

This is a widely distributed western North American polylectic species having been recorded from Idaho, Utah, Nevada, New Mexico, Arizona, California, and Mexico (Baja California). It visits a wide variety of flowers for pollen and nectar. Cockerell (1916a) has recorded it from *Helianthus lenticularis* (as *Halictus helianthi*). It is considered by us to be a casual polylege of *Helianthus*.

62. *Dialictus veganus* (Cockerell)

This western species, ranging from Colorado to New Mexico and southern California has been reported at flowers of *Helianthus* sp. (1♀) in Los Angeles County, California (Moldenke and Neff, 1974). It is judged to be a casual polylege of *Helianthus*.

63. *Dialictus versatus* (Robertson)

This is a highly polylectic species which has been recorded from *Helianthus annuus* (♀P), *H. divaricatus* (♂), *H. grosseserratus* (♀P), *H. mollis* (♀P), and *H. rigidus* (♀P) in Illinois by Robertson (1929). It collects pollen from a wide variety of plants and is a casual polylege of *Helianthus*. It is an eastern North American species ranging from southern Canada (Ontario) to Minnesota and south to Georgia and Louisiana.

64. *Dialictus zephyrus* (Smith)

This species is also highly polylectic and the female has been reported taking pollen from *Helianthus tuberosus* (Robertson, 1929). It occurs from the New England states to Ontario, Minnesota, Colorado, Georgia, and Texas. Much is known about the biology of this species (Hurd, 1979: 1973). It is a casual polylege of *Helianthus*.

Genus *Sphecodes* Latreille

This is a large and nearly worldwide genus of parasitic bees. The majority of the species belong to the nominate subgenus, which is the only group present in America north of Mexico (Michener, 1978). While most of the species are cleptoparasites in the nests of other Halictidae, some are parasitic in the nests of certain species of Andrenidae, Anthophoridae, Colletidae, and Melittidae. Doubtless other species of *Sphecodes* will be found to visit the flowers of *Helianthus* perhaps in company with their host species.

65. *Sphecodes dichrous* Smith

Viereck (1916) has recorded this parasitic bee from sunflower in Connecticut. The species ranges from Nova Scotia to Georgia, Missouri, and Minnesota. It is known to be cleptoparasitic in the nests of *Halictus rubicundus* (Christ), a casual polylege of *Helianthus*.

Family MELITTIDAE

With the exception of the subfamily Ctenoplectrinae, which is found only in the Ethiopian, Oriental, and Australian regions, this family is represented in North America by three subfamilies (Melittinae, Dasypodinae, and Macropodinae) also present in the Eastern Hemisphere. None of these is known to occur in the Neotropical Region, but the Dasypodinae, which contains *Helianthus*-visiting species, is represented by about 20 species in the United States and adjacent northern Mexico. Of these, only two species of the genus *Hesperapis* have been found at the flowers of *Helianthus*. Like most members of this family, these species appear to have evolved as oligoleges and are considered to be important pollinators of sunflowers.

Genus *Hesperapis* Cockerell

There are about 20 species of this genus known from North America and nearly all of these are centered in the more arid parts of the southwest-

ern United States and northern Mexico. Only the two species discussed below have established a known relationship with *Helianthus*.

1. *Hesperapis (Panurgomia) arenicola* Crawford

This species has been recorded from *Helianthus niveus* in San Bernardino County, California (11 males, 2 females), by Moldenke and Neff (1974). Also, in the Timberlake collection there are 11 males and two females collected by P. H. Timberlake from *H. niveus* in Riverside County, California, as follows: Mecca (near), 1♂, 19 Mar 20; Indio (near), 10♂, 1♀N, 18 Mar 27; Indio (5 mi W), 1♀N, 25 Mar 36.

Stage (1966) investigated the floral relationships of this species on the basis of museum collections and reports that the majority of the specimens have been taken at the flowers of the vernal composite, *Geraea canescens*, from which the only females bearing pollen have been collected. He notes that the species has also been found to visit the flowers of *Baileya pleniradiata*, *Dysodia*, *Encelia californica*, *E. farinosa*, *Helianthus niveus*, *Lycium parishii*, *Melilotus*, *Oenothera deltoides*, *Phacelia crenulata*, and *Rafinesquia neomexicana*. He suggests that the species is an oligolege of *Geraea canescens*. Thus most of the floral records pertain to the Compositae and in the absence of detailed field studies we consider this species to be an oligolege of the Compositae secondarily associated with *Helianthus*.

Hesperapis arenicola is known to occur on the Mojave and Colorado deserts being found thus far from Nevada (Clark County), California (Imperial, Riverside, San Bernardino, and San Diego counties), Arizona (Yuma County), and Mexico (Baja California Norte and Sonora).

2. *Hesperapis (Panurgomia) carinata* Stevens

Stage (1966) records this species from North Dakota, Nebraska, Kansas, Utah, Nevada, Oregon, and Idaho. He states that *H. carinata rodecki* Cockerell, originally described from Colorado, is a different species and so treats it in his revision

of this group. *H. carinata* was described from males taken at flowers of *Helianthus scaberrimus* and *H. petiolaris* at Sheldon, North Dakota (Stevens, 1919). Subsequently, Stevens recorded females from flowers of *H. petiolaris* at the same locality. Stage (1966) lists the floral records from museum specimens that indicate that *H. carinata* has most frequently been collected from the flowers of *Helianthus* (*H. annuus*, *H. lenticularis*, *H. petiolaris*, and *H. scaberrimus*), but it has also been taken at the flowers of *Chrysothamnus viscidiflorus* (males and females) and *Cucurbita* (a male). Stage (1966) notes, however, that at two sites in Nevada, *H. carinata* exclusively visited the flowers of *Helianthus* for pollen and nectar even though two other composites (*Chrysothamnus nauseosus* and *Haplopappus lanceolatus*) were in bloom nearby.

It appears that *H. carinata* is an oligolege of the Compositae primarily associated with *Helianthus*.

Family MEGACHILIDAE

This is one of the largest families of bees and more than 100 species have been found to visit the flowers of *Helianthus*. The majority of these are pollen-collecting bees (87 species), but a number of cleptoparasitic species (16) have also been taken at the flowers, sometimes in company with the pollen-collecting species in whose nests they are parasitic. Of the pollen-collecting species, the family is represented by one species of Lithurginae and 86 species of Megachilinae including 14 species of Anthidiini and 72 species of Megachilini (one-third of which are osmiines). While the majority of the pollen-collecting species of Megachilidae that visit sunflowers are polyleges or nectar seekers (65 species), a significant number of species (22) are oligoleges of the Compositae either primarily associated with *Helianthus* (4 species) or secondarily so (18 species). Unquestionably the bees of this family are of much importance as pollinators of sunflowers.

Genus *Lithurge* Latreille

Only 6 species of this genus, which is found in both the Western and Eastern Hemispheres, are

present in North America. Of these, as is discussed below, a single species has been found visiting sunflowers, apparently for nectar since our species are presumably all oligoleges of the Cactaceae.

1. *Lithurge (Lithurgopsis) gibbosus* (Smith)

This is a southeastern cactus oligolege ranging from North Carolina to Florida and Texas. Mitchell (1962) provides some additional flower records, including *Helianthus*, which was presumably being visited for nectar.

Genus *Heteranthidium* Cockerell

This is a North American genus containing 11 species, four of which are oligoleges of Compositae either primarily associated with *Helianthus* (3 species) or secondarily so (1 species). It seems possible that some of the other species of this genus for which we have incomplete or no intrafloral information may be found to be associated with sunflower. Insofar as is known, the species of this genus tend to be oligoleges, for example, *H. bequaerti* Schwarz on *Dalea spinosa*, and *H. larreae* (Cockerell) on *Larrea tridentata*.

2. *Heteranthidium cordaticeps* Michener

This striking but rarely encountered species was described originally from three females, one of which was taken at Austin, Texas (Michener, 1949). Males have since been recorded from New Mexico and southeastern Arizona (Snelling, 1975). One male was taken on *Helianthus annuus*, 0.5 miles north of Apache, 4 September 1972 (Snelling), and a second on either *H. annuus* or *Heterotheca subaxillaris*, 1020-1050, at Apache, Cochise County, Arizona, 24 August 1969 (T. J. Zavortink). Details of the collection of this species at sunflower in Rodeo, New Mexico, are given in Table C.

The species is apparently an oligolege of the Compositae primarily associated with *Helianthus*.

3. *Heteranthidium occidentale* (Cresson)

A female was taken from *Helianthus lenticularis* on 29 August 1907 in Colorado by Cockerell (1907a). The species is known from Colorado, New Mexico, and southern Mexico (Puebla). Since some related species of *Heteranthidium* are primarily associated with sunflower, we have tentatively classed *H. occidentale* as an oligolege of the Compositae primarily associated with *Helianthus*.

4. *Heteranthidium timberlakei* Schwarz

Heteranthidium timberlakei has been taken on a number of composites in Riverside County, California, including *Helianthus gracilentus* (Grigarick and Stange, 1968). It also visits other flowers such as *Clarkia* and *Salvia* (but presumably for nectar) and ranges from Oregon to southern California and western Nevada. It appears to be an oligolege of Compositae secondarily associated with *Helianthus*.

5. *Heteranthidium zebratum* (Cresson)

Recorded by Mitchell (1962) from *Helianthus* and *Gaillardia*, this species ranges from Michigan south to Mississippi and west to South Dakota, Nebraska, Colorado, and New Mexico. Swenk (1914) records it from *H. annuus*, *H. petiolaris*, and *H. subrhomboides* in Nebraska, Cockerell (1909) at *H. pumilus* at Boulder, Colorado, and Michener (1947) at *H. radula* in Mississippi. The species is evidently an oligolege of Compositae primarily associated with *Helianthus*.

Genus *Paranthidium* Cockerell and Cockerell

Included in this genus are three North American species. Only one of these, *P. jugatorium*, is known to be associated with sunflowers, but nothing is known about the floral relationships of *P. sonorum* Michener (Arizona and northern Mexico) and *P. macrurum* (Cockerell) described from Guerrero, Mexico.

6. *Paranthidium (Paranthidium) jugatorium* (Say)

Paranthidium (P.) jugatorium is apparently largely oligolectic on *Helianthus*. Although treated as "species" by Schwarz (1926), four subspecies are currently recognized: *P. jugatorium jugatorium* (New York and New Jersey to Minnesota and Nebraska), *P. j. lepidum* (Cresson) (Kentucky and Virginia to Georgia), *P. j. perpictum* (Cockerell) (Colorado, New Mexico, and Arizona), and *P. j. butleri* Snelling (Arizona). The first of these has been recorded from *Helianthus strumosus* in New Jersey (Schwarz, 1926) and Wisconsin (♂, ♀P) (Graenicher, 1909) and from *H. divaricatus* in Nebraska (Swenk, 1914). *Paranthidium j. perpictum* was reported at *Helianthus* in Boulder, Colorado, by Cockerell (1941b). Females of *P. j. butleri* were collected from the flowers of *Helianthus* and *Erigeron* in the Chiricahua Mountains, Arizona, at elevations ranging from 7000 to 8000 ft in September (Snelling, 1962). The species appears on the basis of current information to be an oligolectic of Compositae secondarily associated with *Helianthus*.

Genus *Anthidium* Fabricius

This genus is represented by numerous species in the Old World as well as on the North and South American continents. Of the 25 species present in America north of Mexico, only the three species discussed below have been taken at the flowers of *Helianthus* and only one of these (*A. paroselae*) is known to collect pollen from these flowers.

7. *Anthidium (Anthidium) maculosum* Cresson

Anthidium maculosum ranges through the western states (South Dakota and Texas west to Oregon and California) into northern Mexico. Its pollen preferences are not known but it has been captured at a variety of plants representing several families, mainly Compositae and Leguminosae (Grigarick and Stange, 1968; Moldenke and Neff, 1974). Parker and Bohart (1966) found the species

nesting in stems of *Sambucus* in Nevada. Based upon our collections (Tables B, C), both sexes visit *Helianthus* for nectar only.

8. *Anthidium (Anthidium) paroselae* Cockerell

Anthidium paroselae is a polylectic bee ranging across the southwestern deserts from Texas to southern California and Sonora, Mexico. Grigarick and Stange (1968) recorded females from flowers of *Palafoxia*, *Prosopis*, and *Larrea* in southern California, as well as from *Helianthus petiolaris* var. *canescens* (Borrego, San Diego County, California). Hurd and Linsley (1975) found it widespread at flowers of *Larrea tridentata* from Las Cruces, New Mexico, to Palm Springs, California, and Hurd (1979) considers the species to be polylectic, listing additional floral information. It nests in hard sand and has two flight periods, one in the spring and one in the autumn. The species is a casual polylectic of *Helianthus*.

9. *Anthidium (Anthidium) porterae* Cockerell

Recorded from *Helianthus petiolaris* in Nebraska (Swenk, 1914), this species occurs from British Columbia, Montana, Wyoming, Colorado, and Nebraska to Arizona, New Mexico, and Texas. Females in our limited samples at *H. annuus* were not taking pollen (Tables B-D). Since this species visits a variety of other flowers including *Asclepias*, *Erigeron*, *Penstemon coloradensis*, *P. occidentata*, *Petalostemon*, *Phacelia distans*, and *Psilostrophe*, its relationship to the flora remains unknown.

Genus *Callanthidium* Cockerell

Included in this genus, which is found only in the western United States and adjacent northern Mexico, are two species, only one of which appears to visit sunflowers.

10. *Callanthidium illustre* (Cresson)

This is a western North American polylectic species ranging from Oregon and Utah south to New Mexico, Arizona, and southern California

to Baja California Norte, Mexico. It has been collected from a wide range of flowers, including *Helianthus*, in California (Grigarick and Stange, 1968; Moldenke and Neff, 1974). Johnson (1904) reported the species nesting in deserted burrows of *Anthophora* in Colorado, Hicks (1929) in dead flower stalks of yucca and oak stumps in southern California and Parker and Bohart (1966) in trap-nests. Its relationship with *Helianthus* is that of a casual polylege.

Genus *Dianthidium* Cockerell

This genus, which also occurs in the Old World, is most abundantly represented by numerous species in the Western Hemisphere. Nineteen species are known to be present in America north of Mexico, of which only three have been taken at sunflowers. Two of these are casual polyleges of *Helianthus* while the third, *D. curvatum* (Smith), is apparently an oligolege of the Compositae, visiting flowers of *Aster*, *Chrysopsis*, *Helenium*, *Helianthus*, *Koellia*, and *Psoralea*.

11. *Dianthidium curvatum sayi* Cockerell

This subspecies, which ranges from Alberta and Idaho to Kansas, Texas, Arizona, and eastern California, has been recorded from flowers of *Helianthus annuus* at Albuquerque, New Mexico, by Cockerell (1898b), from *Helianthus* sp. in Boulder, Colorado, by Cockerell (1914b), from *H. annuus*, *H. petiolaris*, and *H. maximiliani* in Nebraska by Swenk (1914), and from *H. annuus* in North Dakota by Stevens (1949c), who reported both sexes common on sunflowers at a site in Slope County, where they were very inactive, sucking nectar from the flowers and resting on the leaves. An additional record is as follows:

CALIFORNIA.—INYO COUNTY: 15 mi N of Bishop, 5 Aug 48, *H. sp.*, ♂, ♀P (P. D. Hurd, Jr., and J. W. MacSwain).

This subspecies has been found nesting in aggregations in the soil and uses resin from the stems and leaves of *Helianthus petiolaris* for nest construction (Hicks, 1926; Custer and Hicks, 1927; Fischer, 1951).

Although *D. c. sayi* has thus far been taken only at the flowers of *Helianthus*, the nominate subspecies is not known to visit *Helianthus* despite the fact that it visits several other composites. Because of this and since no floral information is available for the subspecies *D. c. xerophilum* Cockerell, we regard *D. c. sayi* as an oligolege of the Compositae secondarily associated with *Helianthus*.

12. *Dianthidium dubium dilectum* Timberlake

Grigarick and Stange (1968) report a female of this subspecies visiting *Helianthus* at Tanbark Flat, Los Angeles County, California, and Moldenke and Neff (1974) record a male at *Helianthus gracilentus* in San Diego County, California. It is primarily confined to central and southern California and is polylectic, visiting a wide variety of flowers (see Hurd, 1979). It is apparently a casual polylege of *Helianthus*.

13. *Dianthidium ulkei* (Cresson)

The nominate subspecies was recorded from *Helianthus petiolaris* in Nebraska by Swenk (1914) and in California by Grigarick and Stange (1968). This subspecies occurs from British Columbia, Montana, and South Dakota south to California, Nevada, Utah, New Mexico, and Nebraska. Although it visits a wide variety of flowers (Hurd, 1979), it is possibly an oligolege of the Compositae, but is evidently only a casual visitor to *Helianthus*. No floral data are available for the subspecies *D. u. cooleyi* Schwarz, known only from Montana. The subspecies *D. u. perterritum* Cockerell, known from Nebraska, New Mexico, and Arizona, has been investigated by Linsley and Hurd (1959) near Portal, Arizona. They report on the mating habits of this subspecies and comment that it was very abundant on flowers of *Haplopappus gracilis*, *Aster tanacetifolius*, *Helianthus*, and *Heterotheca subaxillaris*. Thus, like the nominate subspecies, *D. u. perterritum* appears to be an oligolege of Compositae but its role at the flowers of *Helianthus* is not thoroughly understood.

Pending further field investigations we have

elected to classify *D. ulkei* as a casual polylege of *Helianthus*.

Genus *Anthidiellum* Cockerell

Species of this genus occur on all continents. Two of the three species present in America north of Mexico have been found visiting *Helianthus* as casual polyleges.

14. *Anthidiellum notatum notatum* (Latreille)

Mitchell (1962) includes *Helianthus* among the several plant genera listed as hosts for this subspecies. It is thus a casual polylege of *Helianthus*. It ranges from Massachusetts west to Illinois and south to Florida and Mississippi. Its flight period is reported as April to September. The mating behavior has been described by Turell (1976). Other subspecies are known from western North America, but have not been found visiting sunflowers.

15. *Anthidiellum perplexum* (Smith)

Graenicher (1930) recorded this species at flowers of *Helianthus debilis* in Florida. Turell (1976) described the mating behavior on other plants. The species ranges from North Carolina to Florida and visits a number of flowers many of which are Compositae (Mitchell, 1962). It appears to be a casual polylege of *Helianthus*.

Genus *Dioxys* Lepeletier and Serville

The bees of this Holarctic genus are cleptoparasites in the nests of other megachilids. Five species are present in the Nearctic Region, two of which have been collected at the flowers of *Helianthus*.

16. *Dioxys aurifuscus* (Titus)

A western species ranging from Oregon and Idaho to Colorado and southern California, it is a cleptoparasite of *Callanthidium illustre* Cresson and possibly also *Anthidium maculosum* Cresson.

Hurd (1958) lists a female at flowers of *Helianthus* sp. in southern California.

17. *Dioxys pomonae pomonae* Cockerell

This is a western subspecies ranging from Oregon and Idaho to New Mexico, Arizona, and southern California except the Sonoran Desert. It is cleptoparasitic in the nests of certain species of *Anthidium*, *Chalicodoma*, and *Osmia*. Hurd (1958) records both sexes from flowers of *Helianthus* in southern California.

Genus *Heriades* Spinola

Species of this genus occur in the Ethiopian, Oriental, and Holarctic Regions and are intrusively represented in the Neotropical Region (as far south as Panama). Eleven species are present in America north of Mexico and three of these have been found visiting the flowers of *Helianthus*, one as a regular polylege and two as casual polyleges.

18. *Heriades (Neotrypetes) variolosa variolosa* (Cresson)

The nominate subspecies ranges from Maine and Ontario to Florida and west to British Columbia, Washington, Oregon, Utah, New Mexico, Texas, and northern Mexico. Although a variety of flowers are known to be visited, most records involve Compositae, including *Helianthus* (Hurd and Michener, 1955). This subspecies appears to be a regular polylege of *Helianthus*.

19. *Heriades (Physostetha) carinata* Cresson

Heriades carinatus is widely distributed from coast to coast in southern Canada and the United States, and a wide variety of hosts have been recorded (Hurd and Michener, 1955; Mitchell, 1962), including *Helianthus* at Logan, Utah. The females are polylectic. Among the flowers listed for Wisconsin by Graenicher (1909) is *H. strumosus*, from which females were taking pollen, and by Medler and Lussenhop (1968), *Helianthus* sp. The

nesting habits have been described by Matthews (1965) and Krombein (1967). It is a casual polylege of *Helianthus*.

**20. *Heriades (Physostetha) occidentalis*
Michener**

Heriades occidentalis is a west coast species known from Oregon and California. Apparently polylectic, it has been reported from *Helianthus* sp. in Los Angeles County and *H. gracilentus* in San Diego County, California, by Moldenke and Neff (1974). We regard it as a casual polylege of *Helianthus*.

Genus *Chelostomopsis* Cockerell

This is a monotypic genus and is known only from the western United States.

21. *Chelostomopsis rubifloris* (Cockerell)

Recorded from *Helianthus* in southern California by Hurd and Michener (1955), the species is highly polylectic and ranges from Washington to California, but is also known from two localities in Arizona. It is a casual polylege of *Helianthus*.

Genus *Hoplitis* Klug

Although many species of this genus are present in the Holarctic and Ethiopian Regions, only 24 species are known from the Western Hemisphere (one introduced from Europe) where they are restricted to the Nearctic Region. Seven of these species have been associated with the flowers of *Helianthus*, five as casual polyleges, one as a regular polylege, and one as a nectar-seeking species.

22. *Hoplitis (Andronicus) cylindrica* (Cresson)

Females of *H. cylindrica* were reported gathering pollen from *Helianthus strumosus* in Wisconsin by Graenicher (1909). This species is polylectic, and visits flowers of many families, principally Leguminosae, Compositae, and Labiatae. It ranges from Quebec and Nova Scotia to Florida, west to

Northwest Territories, British Columbia, Colorado, and Texas. It is a casual polylege of *Helianthus*.

**23. *Hoplitis (Dasyosmia) biscutellae*
(Cockerell)**

A male of this species was recorded by Moldenke and Neff (1974) from *Helianthus niveus* in Imperial County, California. It ranges from Texas to southwestern Utah, Nevada, and southern California, and is an oligolege of *Larrea tridentata* (Hurd and Linsley, 1975).

24. *Hoplitis (Alcidamea) pilosifrons* (Cresson)

Recorded from *Helianthus petiolaris* in North Dakota (Stevens, 1949b), this species is found from Quebec and Massachusetts to Florida and west to Alberta, Colorado, and Texas. Michener (1955), who reports that it excavates its nest in the pithy stem of *Helianthus tuberosus*, observed the species to store pollen of *Amorpha fruticosa* and *Melilotus* in its cells. *H. pilosifrons* is a polylectic species that appears to be a casual polylege of *Helianthus*.

25. *Hoplitis (Alcidamea) producta* (Cresson)

Six subspecies are currently recognized. *Hoplitis producta producta* has been recorded from *Helianthus* sp. in Wisconsin, along with other flowering plants, by Medler (1961) and Medler and Lussenhop (1968). *Hoplitis producta interior* Michener has been taken on *Helianthus petiolaris* in Colorado and *H. producta bernardina* Michener on *Helianthus* sp. in southern California (Hurd and Michener, 1955). The species as a whole is polylectic and occurs in southern Canada and throughout the United States except along the southern border and the desert areas. It appears to be a regular polylege of *Helianthus*.

26. *Hoplitis (Alcidamea) sambuci* Titus

Hoplitis sambuci is a polylectic bee occurring from British Columbia and Idaho to California,

Nevada, and Utah. Hurd and Michener (1955) reported it from flowers of many plant species, including *Helianthus*, in southern California. It evidently is a casual polylege of that plant. Clement and Rust (1976) have provided information on the nesting habits of this species.

27. *Hoplitis (Alcidamea) truncata* (Cresson)

The female of this species has been recorded as taking pollen from *Helianthus divaricatus* in Illinois by Robertson (1929). It is apparently polylectic and visits a wide variety of flowers including *Baptisia*, *Berlandiera*, *Ceanothus*, *Cleome*, *Convolvulus*, *Erigeron*, *Gillenia*, *Ilex*, *Melilotus*, *Oenothera*, *Penstemon*, *Pogonia graminifolia*, *Rubus*, *Tephrosia virginiana*, *Trifolium*, *Vaccinium*, and *Vicia*. *Hoplitis truncata* ranges from Quebec and Maine to Florida and west to North Dakota, Wyoming, Colorado, and Arizona. It appears to be a casual polylege of *Helianthus*.

28. *Hoplitis (Robertsonella) simplex* (Cresson)

Graenicher (1909) has reported females of this species gathering pollen from *Helianthus strumosus* in Wisconsin. It may be that this record is a misidentification of *H. gleasoni* (Titus) since *H. simplex* ranges from Texas to Connecticut (Mitchell, 1962). Both of these species, and also *H. micheneri* Mitchell, occur in the eastern United States, but there are no recent records for any of these species from Wisconsin. In any case, whichever species is involved apparently is a casual polylege of *Helianthus*.

Genus *Anthocopa* Lepeletier

This rather large genus of chiefly Holarctic bees occurs in Eurasia, Africa, and western North America (west of the Great Plains). Only a single species of the more than two dozen that occur in North America has been found at the flowers of *Helianthus*. As is discussed below, this species is apparently an oligolege of Compositae secondarily associated with *Helianthus*.

29. *Anthocopa (Eremosmia) hemizoniae* (Cockerell)

This species was originally described from a female taken at flowers of *Helianthus* in Riverside County, California. The male has been taken at *Helianthus gracilentus* by P. H. Timberlake (Hurd and Michener, 1955) and the female is known to visit flowers of *Hemizonia paniculata*. Since the species may be an oligolege of the Compositae, we have classed it as secondarily associated with *Helianthus*.

Genus *Ashmeadiella* Cockerell

This Nearctic genus is represented in America north of Mexico by 50 species, the majority of which are centered in the more arid parts of the southwestern United States and adjacent Mexico. Many of the species have evolved a specialized relationship with the flora and oligolecty is a relatively common phenomenon. However, only four species are known to visit the flowers of *Helianthus* and only two of these are oligoleges of the Compositae secondarily associated with *Helianthus*. Of the remaining two species, one is a casual polylege of *Helianthus* and the other visits the flowers for nectar only.

30. *Ashmeadiella (Ashmeadiella) buconis* (Say)

This species, which includes two subspecies, is an oligolege of Compositae secondarily associated with *Helianthus*.

The nominate subspecies occurs in the central United States (North Dakota south to New Mexico and Texas and east to Wisconsin, Illinois, Indiana, Missouri, and Arkansas) and has been collected on *Helianthus divaricatus* in Illinois by Robertson (1929); and it is reported as taking pollen on *H. sp.* in Nebraska and on *H. petiolaris* in Kansas (Hurd and Michener, 1955). Mitchell (1962) also records this bee as visiting *Helianthus* and Robertson (1929) provides other flower records, mostly *Helianthus* and Astereae.

Ashmeadiella buconis denticulata (Cresson) has

been taken on *Helianthus* in Arizona, Nebraska, and in Modoc County, California (Hurd and Michener, 1955). This subspecies occurs primarily west of the Rocky Mountains from British Columbia southward to southern California and Arizona, but extends eastward into Montana, Wyoming, Colorado, New Mexico, and western Texas.

This latter subspecies was collected once in our sunflower surveys as follows:

CALIFORNIA.—SAN DIEGO COUNTY: 13 Jun 74, *H. gracilentus*, 1300–1415, 2♀N (AEM, MMM).

31. *Ashmeadiella (Ashmeadiella) californica* (Ashmead)

This species occurs along the Pacific Coast from British Columbia to northern Baja California and in the Rocky Mountain region south to New Mexico. Most of the flower records for females are from Compositae. The subspecies *A. c. sierraeensis* Michener has been taken on *Helianthus* and *Solidago* in Sierra County, California, and *A. c. californica* on *Helianthus* sp. in Los Angeles County (Hurd and Michener, 1955) and on *H. gracilentus* in San Diego County, California (Moldenke and Neff, 1974). The species is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

We have taken this species (a male) in our principal sunflower surveys only once (Table D). An additional collection was made as follows:

CALIFORNIA.—SAN DIEGO COUNTY: Vicinity of Laguna at junction with Highway 8, 13 Jun 74, *H. gracilentus*, 1300–1415, 2♀N (AEM, MMM).

32. *Ashmeadiella (Ashmeadiella) foveata* Michener

This species has been recorded from flowers of *Helianthus gracilentus* in the San Bernardino Mountains of southern California by Hurd and Michener (1955). However, the species is apparently polylectic, occurring from California to Arizona, Nevada, and Utah where it visits a wide variety of flowers. It is apparently a casual polylege of *Helianthus*.

33. *Ashmeadiella (Ashmeadiella) titusi* Michener

A male of this southern California bee has been recorded from *Helianthus gracilentus* in San Bernardino County, California, by Hurd and Michener (1955) who also list the species from flowers of *Lotus scoparius* (females, males) and *Phacelia ramosissima* (females). *Ashmeadiella titusi* is possibly an oligolege of *Lotus*.

Genus *Osmia* Panzer

More than 130 species of this Holarctic genus of bees are known to occur in America north of Mexico. Only eight species have established an intrafloral relationship with *Helianthus*, four as oligoleges of Compositae secondarily associated with sunflowers and four as casual polyleges of these plants. A few species visit sunflowers for nesting materials and thus it is important to distinguish the purpose of such visits when assessing the intrafloral relationships of these bees.

34. *Osmia (Chalcosmia) coloradensis* Cresson

This is a western North American oligolege of Compositae secondarily associated with *Helianthus*. Moldenke and Neff (1974) have recorded females from *Helianthus* sp. in Los Angeles County and *H. gracilentus* in San Diego County, California. Rust (1974) reports the species as common on *Helianthus*, *Aster*, and *Senecio*. The species ranges from Nebraska to Texas and west to British Columbia, Washington, Oregon, California, and northern Mexico.

35. *Osmia (Chalcosmia) texana* Cresson

Rust (1974) records a number of genera in six families as floral hosts for this species. Most are Compositae, including *Helianthus*, but the pollen-gathering relationships of *O. texana* to these is not reported. It appears to be an oligolege of the Compositae secondarily associated with *Helianthus*. *Osmia texana* is primarily a western species but extends to the east coast through Michigan and Ohio to New York.

36. *Osmia (Cephalosmia) californica* Cresson

Although Rust (1974) records this western North American species from plants in a number of genera in several plant families, most are Compositae (including *Helianthus*) and most of his records were from *Cirsium*. The species appears to be an oligolege of the Compositae secondarily associated with *Helianthus*. It occurs from British Columbia to California and east to Montana, Wyoming, and Colorado.

37. *Osmia (Cephalosmia) grinnelli* Cockerell

This is a western species ranging from Idaho to Utah, Nevada, and California. Rust (1974) provides a number of flower records including *Helianthus*. P. H. Timberlake has taken females on *Helianthus gracilentus* in the San Bernardino Mountains of southern California (Lytle Creek and Mill Creek). The species is apparently polylectic to judge from available information and is perhaps only a casual polylege of *Helianthus*.

38. *Osmia (Cephalosmia) montana* Cresson

This is a western North American species, with two recognized subspecies: the nominate form extending from the Rocky Mountain states to eastern Washington, Oregon, and California and *O. m. quadriceps* Cresson from southern Washington to California, Nevada, and southern Arizona (Santa Catalina Mountains). Both subspecies appear to be primarily associated with Compositae. Rust (1974) includes *Helianthus* in his list of genera visited by *O. m. montana* and Timberlake collected *O. m. quadriceps* at the flowers of *H. gracilentus* (males and females) in the San Bernardino Mountains of southern California (Mill Creek) on 18 May 1934.

The species is an oligolege of Compositae secondarily associated with *Helianthus*. This is borne out by analyzed pollen stores reported by Rust (1974), which indicate reliance on the Compositae for pollen including *Balsamorhiza sagittata*, *Cosmos*, *Helianthus annuus*, and *Wyethia amplexicaulis*.

39. *Osmia (Nothosmia) marginata* Michener

Restricted, so far as is known at present, to the Colorado Desert of southern California, this appears to be a polylectic species flying in the spring (Hurd and Linsley, 1975). Moldenke and Neff (1974) have recorded a female from *Helianthus niveus* in San Diego County and Hurd (1979) lists it from *H. annuus* and *H. gracilentus*. For the present, we consider the species to be a casual polylege of *Helianthus*.

40. *Osmia (Chenosmia) clarescens* Cockerell

This is a species of the southwestern deserts from New Mexico to southern California. It is polylectic, flying in the spring (Hurd and Linsley, 1975). Moldenke and Neff (1974) record a female from *Helianthus gracilentus* in San Bernardino County, California. It is evidently a casual polylege of *Helianthus*.

41. *Osmia (Diceratosmia) subfasciata subfasciata* Cresson

This polylectic form ranges along the Atlantic Coast to Florida and west to the deserts of southern California (Owens Valley to the southern Colorado Desert) and northern Mexico. It was recorded from *Helianthus* at Falfurrias, Texas, by Cockerell (1914b). It is apparently a casual polylege of *Helianthus*.

Genus *Megachile* Latreille

This genus, which is nearly cosmopolitan in distribution, is represented in America north of Mexico by 115 species. More than 40 of these have been found at the flowers of *Helianthus* with only nine species being oligoleges of the Compositae either primarily (1 species) or secondarily (8 species) associated with *Helianthus*. The remaining species are polyleges (27) or nectar seekers (5). Nonetheless, as is readily apparent in Plate 1 and the Frontispiece, these bees, possibly because of their behavior on the flower, become liberally dusted with pollen (both females and males) and such pollen is available to effect pollination.

42. *Megachile (Litomegachile) brevis* Say

Megachile brevis occurs throughout the United States and Canada and is highly polylectic, visiting a wide variety of plants in many families, especially Compositae, Leguminosae, and Labiatae, including *Helianthus* (Viereck, 1916; Stevens, 1949b; Mitchell, 1962). Robertson (1894, 1922, 1929) regarded it as one of the most regular visitors to *Helianthus* in Illinois, where he found it at five local species of sunflower, *H. divaricatus* (♀N), *H. grosseserratus* (♂,♀P), *H. mollis* (♂), *H. rigidus* (♂) and *H. tuberosus* (♀N). In Wisconsin, Graenicher (1909) found the female taking pollen from *H. strumosus*. Michener (1953) provides an excellent account of the biology of the species. He gives a number of flower records, but *Helianthus* is not included, although he reports the females nesting in dried stems of sunflower, along with other weeds and in other sites. In California females have been recorded from *Helianthus* sp. in Orange County and from *H. annuus* in Riverside County (Moldenke and Neff, 1974). These authors also report the subspecies *M. b. onobrychidis* Cockerell from *Helianthus* sp. in Fresno County. In the southeastern United States, along the coastal plain from North Carolina to Florida and the Gulf Coast to Mississippi and Georgia, the subspecies *M. b. pseudobrevis* Mitchell has also been recorded from *Helianthus* (Mitchell, 1962).

The species is a regular polylege of *Helianthus*.

For collecting records from principal sampling sites, see Tables B, I, and M. It has also been taken from sunflower as follows:

CALIFORNIA.—KERN COUNTY: Bakersfield 8 mi S on Highway 99, 22 Aug 76, *H. annuus*, 1030-1059, 1♂ (AEM, MMM).

43. *Megachile (Litomegachile) coquilletti* Cockerell

This is a western polylectic species ranging from British Columbia and Idaho to Utah, Arizona, and southern California. Moldenke and Neff (1974) have recorded one individual visiting *Helianthus gracilentus* in Riverside County, California. The species appears to be a casual polylege of *Helianthus*.

44. *Megachile (Litomegachile) gentilis* Cresson

This is a widespread polylectic leaf-cutter bee occurring from Texas to California, Nevada, Oregon, and Idaho (it is adventive in Hawaii). Butler (1965) records it from *Helianthus* in Arizona; Moldenke and Neff (1974) report females from *Helianthus* sp. in Kings County and *H. annuus* in Riverside County, California. The life history and nesting habits have been summarized by Krombein (1967). The species apparently visits the flowers of *Helianthus* for nectar only.

In our samples, we have not found females taking sunflower pollen. In addition to the record in Table D, it has been collected as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830-0859, 2♀N (EGL, JML). PINAL COUNTY: Eloy, 14 Jun 74, *H. annuus*, 123-1259, 1♀N (AEM, MMM).

45. *Megachile (Litomegachile) lippiae* Cockerell

This is another widespread polylectic species ranging from Montana and Nebraska to Texas, New Mexico, Arizona, and California. Butler (1965) includes *Helianthus* in his list of flower records for Arizona. Presumably the species is a casual polylege of *Helianthus*.

46. *Megachile (Litomegachile) mendica* Cresson

This is a widespread polylectic species which ranges from Ontario and Maine south to Florida and west to South Dakota, Colorado, Arizona, and California. Pollen-collecting females of the nominate subspecies have been collected at *Helianthus strumosus* in Wisconsin by Graenicher (1909) and at *H. annuus* in Illinois by Robertson (1929). Robertson also took the male at *H. divaricatus* and the species has been recorded from flowers of *H. radula* in Mississippi by Michener (1947). Krombein (1967) has described the life history and nesting habits. *Coelioxys sayi* Robertson recorded by Krombein (1967) and Medler and Lussenhop (1968) among the parasites of this species, was taken at the flowers of *Helianthus* by Pearson (1933).

We have taken the male of the subspecies *M. m. snowi* Mitchell, which occurs in Colorado, New Mexico, and Arizona, at sunflower in Cochise County, Arizona (Table D).

The species is a casual polylege of *Helianthus*.

47. *Megachile (Litomegachile) texana* Cresson

Megachile texana is a widespread polylectic species occurring across the United States and southern Canada. Robertson (1929) has recorded the female of this bee taking nectar from *Helianthus* in Illinois. Michener (1947) reported it at sunflower in Mississippi and Butler (1965) in Arizona. It is evidently a casual polylege of *Helianthus*.

Our sampling has yielded only nectar visitors (Table B) and the following accessory records:

ARIZONA.—PIMA COUNTY: Sahuarita, 26 Jun 74, *H. annuus*, 1200-1229, 3♂, 1♀N (AEM, MMM).

48. *Megachile (Cressoniella) zapoteca* Cresson

This is a Mexican and Central American species that extends into southeastern Arizona, where it has been taken on *Helianthus* and several other plants (Butler, 1965). The species is presumably polylectic, having been taken at the flowers *Asclepias*, *Helenium*, *Lathyrus*, *Melilotus*, and *Monarda*. In relationship with *Helianthus* it appears to be that of a casual polylege.

49. *Megachile (Megachile) centuncularis* (Linnaeus)

This is a Holarctic species and obviously polylectic. Males and females taking pollen from *Helianthus strumosus* have been recorded by Graenicher (1909) in Wisconsin. It has also been reported from *Helianthus* by Mitchell (1935) and Stevens (1949b). Krombein (1967) has summarized the known information on the nesting habits and parasites of this species in North America, where it is principally northern, but occurs south to Florida, Missouri, Colorado, Nevada, and Arizona. It apparently is a casual polylege of *Helianthus*.

50. *Megachile (Megachile) inermis* Provancher

Megachile inermis is a wide ranging, polylectic species that occurs from Nova Scotia to Georgia, west to British Columbia, and south to California, Utah, Colorado, New Mexico, and Texas. It has been recorded from *Helianthus* sp. and *H. giganteus* in Wisconsin by Medler (1958a) and Medler and Lussenhop (1968). Its nesting habits are well known, having been described from various localities (for references see Hurd, 1979). It is apparently a casual polylege of *Helianthus*.

51. *Megachile (Megachile) montivaga* Cresson

A widely distributed polylectic species ranging from Nova Scotia to North Carolina, west to Mexico, California and British Columbia, *M. montivaga* has been reported as a visitor to *Helianthus* by Mitchell (1935, 1962), Butler (1965), and Moldenke and Neff (1974). We collected the species only once during our surveys (Table C); in that instance it was taking pollen and nectar from *H. annuus*. It appears to be a regular polylege of *Helianthus*.

52. *Megachile (Megachile) relativa* Cresson

Megachile relativa is a widespread polylectic species having been found from Mackenzie to Newfoundland and south to California, Arizona, Illinois, Tennessee, and Georgia. It has been taken at flowers of *Helianthus giganteus* and *H. grosseserratus* in Wisconsin (Medler and Lussenhop, 1968). Its nesting habits have been described by Medler, (1958b), Medler and Koerber (1958), Mitchell (1962), and Medler and Lussenhop (1968). *Megachile relativa* is apparently a casual polylege of *Helianthus*.

53. *Megachile (Eutricharaea) concinna* Smith

An introduced species from the Palaearctic Region which is now known throughout the United States, *M. concinna* has been recorded from a wide range of pollen and nectar plants but not previously from *Helianthus*.

A single male was taken in our sunflower surveys as follows:

CALIFORNIA.—KERN COUNTY: Bakersfield 9 mi S on Highway 99, 22 Aug 76, *H. annuus*, 1030–1059, 1♂ (AEM, MMM).

**54. *Megachile (Delomegachile) gemula gemula*
Cresson**

This is a widespread polylectic subspecies ranging over most of North America. Medler and Lussenhop (1968) have reported it visiting *Helianthus giganteus* and other flowers in Wisconsin. It appears to be a casual polylege of *Helianthus*.

**55. *Megachile (Delomegachile) melanophaca*
Smith**

Distributed across Canada and the northern United States to Colorado, New Mexico, Arizona, and California, this polylectic species has been recorded from *Helianthus* by Mitchell (1935, 1962) and Butler (1965). It is parasitized by *Coelioxys (Boreocoelioxys) rufitarsis* which has been taken with it at flowers of *Helianthus giganteus* by Medler and Lussenhop (1968) in Wisconsin. It evidently is a casual polylege of *Helianthus*.

56. *Megachile (Phaenosarus) agustini* Cockerell

Megachile agustini has been recorded from *Helianthus annuus* in Colorado by Mitchell (1936) and *Helianthus* and other Compositae in Arizona by Butler (1965). The species occurs in Colorado, Utah, Arizona, and New Mexico and is apparently a casual polylege of *Helianthus*.

In our samples, *M. agustini* is represented in Tables A, C, and D (New Mexico and Arizona).

57. *Megachile (Phaenosarus) fortis* Cresson

Megachile fortis occurs from South Dakota to Arizona and eastward and southward to Illinois, Texas, and Louisiana. Mitchell (1936) lists several collections from *Helianthus*, including *H. petiolaris* and *H. subrhomboides*. The species appears to be polylectic and a regular polylege of *Helianthus*.

58. *Megachile (Derotropis) xerophila* Cockerell

Mitchell (1936) records a female of this species from Borrego Valley, San Diego County, Califor-

nia, 26 March, on *Helianthus niveus*, P. H. Timberlake, collector. The species is known only from the deserts of southern California and Arizona, flying in March, April, and May. It appears to be an oligolege of the Compositae secondarily associated with *Helianthus*.

59. *Megachile (Xeromegachile) alata* Mitchell

This species is principally associated with Compositae in Arizona, southern California, and Baja California Norte, Mexico. Moldenke and Neff (1974) have recorded a male at flowers of *Helianthus gracilentus* in Riverside County, California. To judge from the available floral information, this species is apparently an oligolege of the Compositae secondarily associated with *Helianthus*.

**60. *Megachile (Xeromegachile) casadae*
Cockerell**

The species has been recorded from South Dakota, Nebraska, Oklahoma, Texas, Wyoming, Colorado, New Mexico, Utah, Arizona, and California. Mitchell (1937a) recorded the male from *Helianthus* in Sioux County, Nebraska. The pollen host of the female has not been reported, but the species presumably is a casual polylege of *Helianthus*.

**61. *Megachile (Xeromegachile) coloradensis*
Mitchell**

We have found no published flower records for this species, which previously was known only from Colorado.

Our only collection of this species at sunflower is as follows:

ARIZONA.—PINAL COUNTY: Eloy, 30 Jul 75, *H. annuus*, 1♀N (AEM, MMM).

**62. *Megachile (Xeromegachile) dakotensis*
Mitchell**

This species is recorded from *Helianthus* and other plants, mostly Compositae, by Mitchell (1937a, 1962). It has been collected in Minnesota, Iowa, Illinois, Montana, North and South Dakota, Nebraska, and Texas. The species appears

to be an oligolege of the Compositae secondarily associated with *Helianthus*.

**63. *Megachile (Xeromegachile) manifesta*
Cresson**

The male of *M. manifesta* was recorded from sunflower in Colorado by Mitchell (1937a). The species ranges from Alberta, Montana, and North Dakota to New Mexico, Arizona, and southern California. Most recorded flower hosts are Compositae, including *Helianthus* (Butler, 1965), and the species apparently is an oligolege of the Compositae secondarily associated with *Helianthus*.

We have taken this species on sunflowers in New Mexico (Table A) and in California as follows:

CALIFORNIA.—LOS ANGELES COUNTY: Sunland, Tujunga Canyon, 14 May 75, *H. annuus*, 1230–1259, 3♂, 1♀ (AEM, MMM).

**64. *Megachile (Xeromegachile) nevadensis*
Cresson**

This is a western species occurring from Washington and California east to Montana, Wyoming, Colorado, and New Mexico. It has been associated with a wide range of Compositae. Moldenke and Neff (1974) report it from *Helianthus* in Inyo County, California. It is apparently an oligolege of autumnal flowering Compositae (see Hurd, 1979), but is not known to collect pollen from *Helianthus*.

Our samples included only one specimen as follows:

CALIFORNIA.—SAN DIEGO COUNTY: Vicinity of Laguna Junction and Highway 8, 13 Jun 74, *H. gracilentus*, 1300–1415, 1♂ (AEM, MMM).

65. *Megachile (Argyropile) mucorosa* Cockerell

Mitchell (1934) recorded this species from *Helianthus* in War Bonnet Canyon, Sioux County, Nebraska (as *M. nebraskana* Mitchell) and Butler (1965) recorded it from *Helianthus* in Arizona. It is a species of the Great Plains and southwestern United States and occurs from Nebraska and

Kansas to Wyoming, Colorado, Utah, Arizona, New Mexico, and Texas.

One example was taken in our surveys as follows:

ARIZONA.—SANTA CRUZ COUNTY: Sonoita, 16 Aug 74, *H. annuus*, 1♀N (PDH, AEM, MMM).

The species has, in addition to *Helianthus*, been collected at the flowers of *Eustoma issenianum*, *Monarda*, and *Ratibida columnaris*. It is judged to be a casual polylege of *Helianthus*.

66. *Megachile (Argyropile) parallela* Smith

FIGURE 6; PLATE 1, FRONTISPIECE

Megachile parallela is transcontinentally distributed in southern Canada and the United States and is found as far south as the Isthmus of Tehuantepec. It has been reported visiting a wide variety of flowers, notably those of the Compositae (Hurd, 1979), but seems to be primarily associated with *Helianthus*. It has been reported from flowers of *Helianthus maximiliani* at Dallas, Texas, by Cockerell (1914b), at *H. annuus lenticularis* in Nebraska by Cockerell (1923), at *H. petiolaris* in Nebraska and Colorado by Mitchell (1937b), and *H. radula* in Mississippi by Michener (1947). In California, both sexes have been recorded from *H. annuus* in Riverside County, from *H. gracilentus* in San Diego County and a female from *H. nuttallii* in Lassen County (Moldenke and Neff, 1974). Records provided by Robertson (1929) including *H. divaricatus* (♀P) and *H. mollis* (♂) suggest a preference for species of Heliantheae and Astereae. The nest has been described by Fischer (1951) and by Medler and Lussenhop (1968).

This primary oligolege of *Helianthus* was taken in most of our principal survey sites (see Tables A–D, F, G, K, L), and also as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800–0859, 2♂, 13♀P, 15♀N (EGL, JML). GRAHAM COUNTY: Franklin, 6 Aug 75, *H. annuus*, 1130–1159, 1♂ (EGL, JML). PIMA COUNTY: Marana, 27 Jun 74, *H. annuus*, 1030–1059, 1♂, 1♀N (AEM, MMM). SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0800–0859, 6♂ (EGL, JML); Patagonia, 7 Sep 77, *H. annuus*, 0730–0759, 1♀P (EGL, JML); Sonoita, 16 Aug 74, *H. annuus*, 4♂ (PDH, AEM, MMM);

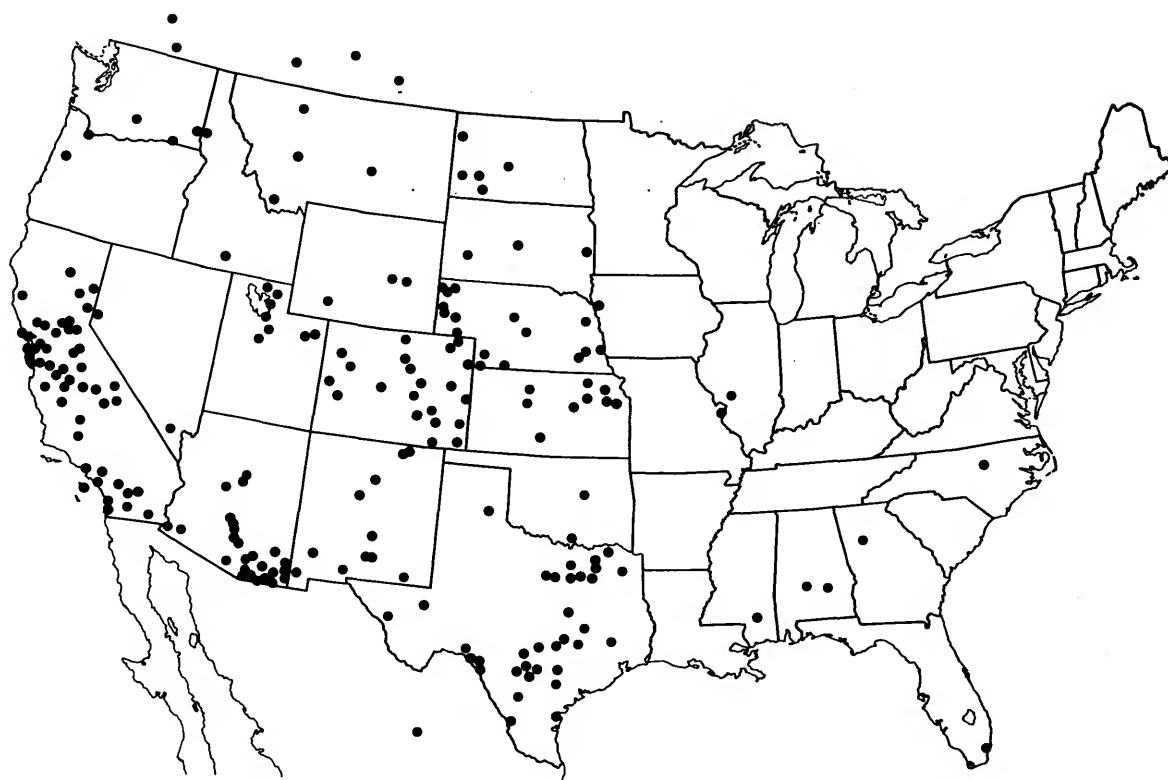


FIGURE 6.—Distribution of *Megachile (Argyropile) parallela* Smith.

Sonoita, 10 mi E, 7 Sep 77, *H. petiolaris*, 0830-0859, 1♂ (EGL, JML). YUMA COUNTY: Tacna, 29 Jul 75, *H. annuus*, 1415-1429, 1♀P (AEM, MMM).

CALIFORNIA.—FRESNO COUNTY: Parlier, 7 Sep 75, *H. annuus*, 1400-1429, 1♀N (EGL, JML, AEM, MMM). IMPERIAL COUNTY: El Centro, 29 Jul 75, *H. annuus*, 1015-1029, 3♂ (AEM, MMM). INYO COUNTY: Tuttle Creek, 4 mi W of Lone Pine, 29 Aug 77, *H. annuus*, 1030-1059, 1♀N (EGL, JML); KERN COUNTY: Bakersfield 8 mi S on Highway 99, 22 Aug 76, *H. annuus*, 1030-1059, 1♂, 1♀N (AEM, MMM). MERCED COUNTY: Atwater, 23 Jul 77, *H. annuus*, 1100-1129, 1♀N (EGL, JML, AEM, MMM). ORANGE COUNTY: Newport Beach, 25 Sep 76, *H. annuus*, 1♂ (AEM, MMM). RIVERSIDE COUNTY: Coachella, 8 Jun 76, *H. annuus*, 0900-0929, 2♂, 4♀P, 3♀N (EGL, JML); Indio, 8 Jun 76, *H. annuus*, 0800-0829, 3♂ (EGL, JML).

67. *Megachile (Argyropile) sabinensis* Mitchell

This species is presently known only from Arizona, New Mexico, and Texas. Butler (1965) has recorded it from *Helianthus*, as well as *Aster*, *Bail-*

eya, *Eriogonum*, and *Haplopappus*. It appears to be an oligolege of the Compositae secondarily associated with *Helianthus*.

68. *Megachile (Argyropile) townsendiana* Cockerell

This species has been recorded from *Helianthus debilis* in Florida by Graenicher (1930) and from *H. sp.* in Arizona by Butler (1965). The species ranges from North Carolina to Florida and west to Oklahoma, Texas, Colorado, New Mexico, Arizona, southeastern California, and northern Mexico. We have encountered it once in our surveys as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830-0859, 1♂ (EGL, JML).

It appears to be a casual polylege of *Helianthus*.

**69. *Megachile (Xanthosarus) dentitarsus*
Sladen**

This species has been recorded from Alberta, Washington, Montana, North and South Dakota, Wyoming, Nebraska, Colorado, Utah, New Mexico, and Arizona. Mitchell (1936) lists it from *Helianthus petiolaris* in Nebraska. It is apparently polylectic, visiting a number of different kinds of flowers, and appears to be a casual polylege of *Helianthus*.

70. *Megachile (Xanthosarus) latimanus* Say

This is a largely northern species ranging from Nova Scotia to Alberta and on the southern extreme from Georgia to Kansas, Colorado, and Wyoming. Robertson (1894, 1922, 1929) classed it as one of the most regular visitors to sunflowers in Illinois, where he found it on all local species, including *Helianthus divaricatus* (♀P), *H. grosseserratus* (♂, ♀P), *H. mollis* (♂, ♀P), *H. rigidus* (♂, ♀N) and *H. tuberosus* (♀N). In Wisconsin, Graenicher (1909) found it at *H. giganteus* (♂) and *H. strumosus* (♂, ♀P). Mitchell (1936, 1962) also recorded it from *Helianthus*, along with other Compositae, a group for which he suggested the bees had preference, and Stevens (1949b) recorded it from *H. maximiliani* and *H. rigidus* in North Dakota and Medler and Lussenhop (1968) from *H. giganteus* and *H. grosseserratus* in Wisconsin.

Megachile latimanus, however, appears to be mainly dependent upon the pollen of a wide variety of other plants (Hurd, 1979) and is judged to be a casual polylege of *Helianthus*.

**71. *Megachile (Xanthosarus) perihirta*
Cockerell**

This species ranges from British Columbia to Mexico and east to Nebraska and Texas (Mitchell, 1962). It has been recorded from *Helianthus annuus* by Mitchell (1936), *H. sp.* in Arizona by Butler (1965) and Moldenke and Neff (1974), who also report females at *H. petiolaris* in Stanislaus County and *H. sp.* elsewhere in California. *Megachile perihirta* is polylectic and evidently is a regular polylege of *Helianthus*.

Our records of this species at sunflower are from coastal southern California:

CALIFORNIA.—LOS ANGELES COUNTY: Pico Rivera, 11 Aug 75, *H. annuus*, 1♂ (AEM, MMM). ORANGE COUNTY: Newport Beach, 21–25 Aug 75, *H. annuus*, 1500–1545, 2♂, 4♀P, 4♀N (AEM, MMM).

72. *Megachile (Leptorachis) petulans* Cresson

This polylectic species visits a wide variety of composites and legumes (Robertson, 1929; Mitchell, 1962) and ranges from New Jersey to Florida and west to North Dakota, Nebraska, — 1 166 Arizona, and Mexico. Robertson (1929) records Arizona, and Mexico. Robertson (1929) records it from the flowers of *H. divaricatus* (♂, ♀P), *H. mollis* (♀N) and *H. strumosus* (♂) in Illinois and Mitchell (1937b) lists it from *H. atrorubens* and *H. sp.* in North Carolina. It appears to be a casual polylege of *Helianthus*.

**73. *Megachile (Pseudocentron) pruina pruina*
Smith**

Mitchell (1937b) recorded this subspecies from *Helianthus* in Florida. It ranges from North Carolina to Florida and also occurs on Bermuda. It is apparently a casual polylege of *Helianthus*.

**74. *Megachile (Pseudocentron) sidalcea*
Cockerell**

Recorded from *Helianthus ciliaris* at Mesilla, New Mexico, by Cockerell (1900) and *H. sp.* in Arizona by Butler (1965), this species ranges from Texas to southern California and Mexico and is generally common throughout its range. It is polylectic and apparently visits *Helianthus* for nectar only.

Our collections of this species from sunflower sampling sites are mostly males, as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Aug 75, *H. annuus*, 8 Aug 75, 0800–0829, 1♀N (EGL, JML). MARICOPA COUNTY: Theba, 28 Jun 74, *H. annuus*, 0955–1200, 4♂, 1♀N (AEM, MMM). PIMA COUNTY: Marana, 27 Jun 74, *H. annuus*, 1030–1059, 1♂ (AEM, MMM), 30 Jul 75, *H. annuus*, 1100–1114 2♂ (AEM, MMM); Sahuarita, 26 Jun 74, *H. annuus*, 1200–1229, 6♂ (AEM, MMM). PINAL COUNTY: Eloy,

14 Jun 74, *H. annuus*, 1130–1159, 1♂ (AEM, MMM). YUMA COUNTY: Tacna, 14 Jun 74, *H. annuus*, 1305–1325, 1♂ (AEM, MMM).

75. *Megachile (Acentron) albitarsis* Cresson

This is a polylectic species ranging from Michigan and Indiana to North Carolina and Florida and west through Texas to Arizona and northern Mexico (Mitchell, 1962). Michener (1947) has recorded it from *Helianthus radula* in Mississippi, Robertson (1894, 1898) from *H. divaricatus* and *H. tuberosus*. It appears to be a casual polylege of *Helianthus*.

76. *Megachile (Melanosarus) xylocopoides* Smith

This polylectic leaf-cutter bee ranges from Maryland to Florida and through the Gulf States to Texas. Cockerell (1900) recorded it from *Helianthus ciliaris* in New Mexico. The life history and parasites have been treated by Krombein (1967). It appears to be a casual polylege of *Helianthus*.

77. *Megachile (Sayapis) fidelis* Cresson

Recorded from *Helianthus petiolaris* by Mitchell (1937b) (locality not specified), from *Helianthus* in Arizona by Butler (1965), and from *H. gracilentus* in southern California, this species ranges from Montana, South Dakota, Nebraska, and New Mexico, west to Idaho, Oregon, and California. It is a polylectic species that appears to be a regular polylege of *Helianthus*.

78. *Megachile (Sayapis) frugalis* Cresson

The nominate subspecies was recorded from *Helianthus* by Butler (1965). Mitchell (1962) gives the range as Pennsylvania and New Jersey to Florida and west to California and Mexico. A female of *M. frugalis pseudofrugalis* taking pollen from *Helianthus gracilentus* was captured by P. H. Timberlake at The Gavilan, Riverside County, California, in June.

Megachile frugalis is a polylectic species whose

relationship with *Helianthus* is judged to be that of a casual polylege.

79. *Megachile (Sayapis) helianthi* Cockerell

This species was described by Cockerell (1908) from material collected from *Helianthus lenticularis* at Boulder, Colorado, and later was again recorded from this plant by Cockerell (1914b). No additional floral information is available. It is possibly an oligolege of the Compositae and may be secondarily associated with *Helianthus*.

80. *Megachile (Sayapis) inimica* Cresson

Three subspecies, *M. (S.) inimica sayi* Cresson (northern), *M. (S.) i. inimica* Cresson (southern), and *M. (S.) i. jacumbensis* Mitchell (California, Baja California) are recognized by Mitchell (1962) and others. The northern subspecies was regarded as one of the most regular visitors to sunflowers in Illinois by Robertson (1894, 1922, 1929) who found it at *Helianthus divaricatus* (♀P), *H. grosseserratus* (♀P), *H. rigidus* (♀P), and *H. tuberosus* (♀P). Mitchell (1937b) included *Helianthus petiolaris* among the flower hosts for *M. inimica* and Medler and Lussenhop (1968) listed it from *Helianthus* spp. in Wisconsin. Butler (1965) recorded two of the subspecies from Arizona, but only *M. inimica sayi* from *Helianthus*. The life histories and nest structures of each subspecies have been described by Krombein (1967).

Megachile inimica is evidently an oligolege of the Compositae secondarily associated with *Helianthus*.

This important pollinator of sunflowers was taken at our primary sampling sites (Tables A–C, K) as well as the following:

ARIZONA.—GRAHAM COUNTY: Franklin, 6 Aug 75, *H. annuus*, 1130–1159, 2♂ (EGL, JML). SANTA CRUZ COUNTY: Sonoita, 16 Sep 74, *H. annuus*, 3♂ (PDH, AEM, MMM).

81. *Megachile (Sayapis) polycaris* Say

Recorded from *Helianthus* by Mitchell (1962) and Butler (1965), this species ranges from Georgia and Florida west to California and south into

Mexico. Krombein (1967) described the nesting habits in Arizona. Pollen analysis revealed that females were storing pollen from mesquite (*Prosopis*). The species, however, is polylectic, especially preferring flowers of the Compositae, and is a regular polylege of *Helianthus*.

Documenting *M. pollicaris* as an important pollinator of sunflowers, data from our collections are available in Tables A–C and G. It was also taken as follows:

ARIZONA.—PIMA COUNTY: Marana, 27 Jun 74, *H. annuus*, 1030–1059, 3♀N (AEM, MMM); San Xavier, 19 Sep 74, *H. annuus*, 1200–1229, 1♂ (AEM and MMM).

CALIFORNIA.—IMPERIAL COUNTY: Holtville 3 mi W, 29 Jul 75, *H. annuus*, 1100–1114, 1♀P (AEM, MMM).

82. *Megachile (Sayapis) pugnata pugnata* Say

Recorded from *Helianthus tuberosus* by Mitchell (1937b), from *H. divaricatus* (♀P) in Illinois by Robertson (1929), from *H. strumosus* (♂, ♀P) by Graenicher (1909) and *H. giganteus* and *H. grosseserratus* in Wisconsin by Medler (1964) and Medler and Lussenhop (1968), this subspecies occurs transcontinentally in the United States and southern Canada, but is absent in the lower Mississippi Valley and Gulf Coast. It is an oligo-lege of the Compositae secondarily associated with *Helianthus*.

We have collected this species at sunflower once as follows:

ARIZONA.—SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0930–0959, 1♀N (EGL, JML).

Genus *Chalicodoma* Lepeletier

This genus, which is represented in North America by two subgenera, also contains a number of subgenera in the Old World and one in South America. Nineteen species are known from America north of Mexico, of which seven visit sunflowers, two as casual polyleges and the others as nectar visitors.

83. *Chalicodoma (Chelostomoides) angelarum* (Cockerell)

This species occurs from British Columbia to southern California, Nevada, and Arizona, exclu-

sive of the desert areas. The females are polylectic and visit a wide variety of plants for pollen. Moldenke and Neff (1974) report a female at *Helianthus* sp. in Stanislaus County and a male at *H. gracilentus* in San Diego County, California.

In addition to the record in Table K, one example was taken in the sunflower surveys as follows:

CALIFORNIA.—KERN COUNTY: Bakersfield 8 mi S on Highway 99, 22 Aug 76, *H. annuus*, 1030–1059, 1♀N (AEM, MMM).

The species is evidently only a casual polylege of *Helianthus*.

84. *Chalicodoma (Chelostomoides) campanulae campanulae* (Robertson)

Medler and Lussenhop (1968) provide a number of flower records for this species in Wisconsin, including *Helianthus* sp. The nesting habits have been reported by Medler (1966), Medler and Lussenhop (1968), Krombein (1967), and others. It ranges from Quebec and Massachusetts to Florida and west to Iowa, Wisconsin, Minnesota, Nebraska, Kansas, and Texas. It appears to be polylectic and presumably is a casual polylege of *Helianthus*. The other subspecies, *C. c. wilmingtongi* (Mitchell) occurs along the coastal areas from Virginia to Florida but is not known to visit sunflowers.

85. *Chalicodoma (Chelostomoides) chilopsidis* (Cockerell)

Chalicodoma chilopsidis was reported as a visitor to *Helianthus* in Arizona by Butler (1965). It is a southwestern species ranging from Texas to southern California and northern Mexico taking pollen primarily from flowering desert trees and shrubs, especially Leguminosae. It presumably visits *Helianthus* only for nectar.

86. *Chalicodoma (Chelostomoides) occidentalis* (Fox)

This species ranges across the southwestern deserts from western Texas to southern California. It is polylectic and is often found at flowering

trees and shrubs. Butler (1965) has recorded it from *Helianthus* in Arizona.

Our records, based upon casual nectar visitors, may be found in Tables C and F and as follows:

ARIZONA.—PIMA COUNTY: San Xavier, 19 Jun 74, *H. annuus*, 1200–1229, 2♀P (PDH, AEM, MMM).

It thus appears to seek only nectar from sunflowers.

87. *Chalicodoma (Chelostomoides) odontostoma* (Cockerell)

Butler (1965) recorded this species as a *Helianthus* visitor in Arizona. It occurs in the deserts of southern California, Arizona, New Mexico, and northwestern Mexico, primarily at flowering trees and shrubs, but it has also been taken at annuals presumably questing for nectar.

88. *Chalicodoma (Chelostomoides) spinotulata* (Mitchell)

This species is a polylege especially of desert trees and shrubs. It occurs through the southwestern deserts from western Texas to southern California. The male has been reported at *Helianthus* sp. in Los Angeles County, California, by Moldenke and Neff (1974).

89. *Chalicodoma (Chelostomoides) subexilis* (Cockerell)

This species ranges from Nebraska, Colorado, and Utah, south to New Mexico, Arizona, and California. It has been reported as a visitor to flowers of *Helianthus* at Boulder, Colorado, by Mitchell (1937b). It has been recorded from a variety of flowering plants and is apparently polylectic.

Genus *Coelioxys* Latreille

These bees, which are cleptoparasites primarily in the nests of *Megachile* and relatives, occur on all continents. Nearly 50 species are found in America north of Mexico and a number of these (14 species) have been taken at the flowers of

Helianthus, sometimes in the company of their host species. Doubtless additional species of this genus will be found visiting sunflowers.

90. *Coelioxys (Coelioxys) sodalis* Cresson

Graenicher (1909) records the female of this species at flowers of *Helianthus strumosus* in Wisconsin. The species ranges from Alaska and Canada (N.W.T.), south to California, Arizona, and New Mexico in the west and the Great Lakes and New England states in the east.

91. *Coelioxys (Boreocoelioxys) banksi* Crawford

A male and female have been recorded by Moldenke and Neff (1974) from *Helianthus* without locality data. The species is widespread, ranging transcontinentally from Quebec and North Carolina to British Columbia and south to New Mexico, Arizona, and California.

92. *Coelioxys (Boreocoelioxys) moesta* Cresson

Coelioxys moesta is widely distributed from Alaska to Nova Scotia and southward to Virginia, New Mexico, Arizona, and California. Medler and Lussenhop (1968) include *Helianthus giganteus* among their flower records for Wisconsin.

93. *Coelioxys (Boreocoelioxys) novomexicana* Cockerell

This species ranges from Texas to California and Oregon and southward into northern Mexico. Moldenke and Neff (1974), without locality data, list a male at flowers of *Helianthus* sp.

94. *Coelioxys (Boreocoelioxys) octodentata* Say

Both sexes of this bee have been recorded from *Helianthus strumosus* in Wisconsin by Graenicher (1909) and males from *H. divaricatus* and *H. mollis* in Illinois by Robertson (1929). The species occurs transcontinentally in the United States, southern Canada and south into Mexico.

95. *Coelioxys (Boreocoelioxys) rufitarsus* Smith

This species has been reported at flowers of *Helianthus* in Illinois by Pearson (1933) and more specifically at *H. grosseserratus* (♀) by Robertson (1929). In Wisconsin it has been taken at *H. strumosus* (♂) by Graenicher (1909) and *H. giganteus* by Medler and Lussenhop (1968). Host species for this parasite include *Megachile latimanus* and *M. melanophaea* (Graenicher, 1905) both of which also visit *Helianthus*. The species occurs transcontinentally in the United States, southern Canada and south into Mexico.

96. *Coelioxys (Boreocoelioxys) sayi* Robertson

Coelioxys sayi has been recorded from *Helianthus divaricatus* at Carlinville (Robertson, 1929) and in the Chicago, Illinois, area by Pearson (1933). Graenicher (1909) found the male at *H. strumosus* in Wisconsin. The species occurs from New York to Florida and west to Nebraska, Colorado, and Arizona. It is a parasite of *Megachile (Litomegachile) mendica* (Medler, 1965; Krombein, 1967), which has also been taken at flowers of *Helianthus*.

97. *Coelioxys (Xerocoelioxys) edita* Cresson

This parasitic bee has been recorded from the flowers of *Helianthus annuus* by Mitchell (1973) and by Moldenke and Neff (1974). It is a wide ranging species extending across the continent (Florida, Illinois, Missouri, Arkansas, and Texas, west to Alberta, Washington, Oregon, and California).

Details of the capture of this species at sunflower in the principal sampling sites in New Mexico are given in Tables B and C. In addition, a male was taken as follows:

CALIFORNIA.—RIVERSIDE COUNTY: Indio, 8 Jun 76, *H. annuus*, 0800-0829, 1♂ (EGL, JML).

98. *Coelioxys (Schizocoelioxys) funeraria* Smith

A male of this species was taken on flowers of *Helianthus strumosus* in Wisconsin by Graenicher

(1910a). The species ranges from Alaska, Yukon, and British Columbia east to Nova Scotia, south to Illinois, Indiana, Pennsylvania, and Georgia in the east, and south to California, Utah, and New Mexico in the west. It parasitizes the nests of several species of *Megachile* including *M. latimanus* and *M. relativa*, which also visit sunflowers.

99. *Coelioxys (Synocoelioxys) alternata* Say

Robertson (1929) recorded the capture of a female of this species at *Helianthus divaricatus*. The species ranges from Quebec to North Carolina and west to British Columbia, Washington, Utah, and Arizona. Medler and Lussenhop (1968) report the species to be cleptoparasitic in the nests of *Megachile pugnata*, a species that commonly visits sunflowers.

100. *Coelioxys (Synocoelioxys) texana* Cresson

Graenicher (1909) found the male of this species at *Helianthus strumosus*. Mitchell (1973) also reported this species as a visitor to *Helianthus*. It is a parasite of *Megachile polycaris* (Krombein, 1967), which also visits *Helianthus*. The species occurs from Florida, Missouri, Kansas, Oklahoma, and Texas, west to southern California, and south into Central America.

101. *Coelioxys (Neocoelioxys) menthae* Cockerell

This species is thus far known primarily from Arizona and New Mexico, but it ranges south through Mexico into Central America (San Salvador). Presumably parasitic in the nest of *Megachile*, its host has not been reported. Both sexes seek nectar from a variety of flowers. The capture of a male at *H. annuus* is reported in Table C.

102. *Coelioxys (Glyptocoelioxys) germana* Cresson

This species of *Coelioxys* was reported as a visitor to *Helianthus divaricatus* at Carlinville, Illinois, by Robertson (1929) and *Helianthus* sp. in the Chi-

cago region of Illinois, by Pearson (1933). It ranges from Illinois to New Jersey and south to Florida.

103. *Coelioxys (Cyrtocoelioxys) modesta* Smith

A male was taken at *Helianthus strumosus* by Graenicher (1909) in Wisconsin. The species ranges from Quebec and the New England states west to Nebraska and south into Florida and Texas.

Family ANTHOPHORIDAE

This is one of the largest families of bees and more than 140 species have been found to visit the flowers of *Helianthus*. The majority of these are pollen-collecting bees (109 species), but a number of cleptoparasitic species (35) have also been taken at the flowers, sometimes in company with the pollen-collecting species in whose nests they are parasitic. Of the pollen-collecting species, the family is represented by relatively few Xylocopinae (14 species) but by numerous species of the Anthophorinae (95), many of which are members of the tribe Eucerini (74 species). While the majority of the pollen-collecting species of Anthophoridae that visit sunflowers are polyleges (35 species) or nectar seekers (27 species), a very significant number of species (47) are oligoleges of the Compositae either primarily associated with *Helianthus* (12 species) or secondarily so (35 species). In this regard only the Andrenidae contains more species of oligoleges (50) either primarily associated with *Helianthus* (18) or secondarily so (32). Clearly the bees of this family are of much importance in the pollination of sunflowers.

Genus *Neolarra* Ashmead

The bees of this North American genus are very small-sized cleptoparasites in the nests of *Perdita* and *Nomadopsis*. Fourteen species are known from the United States, only two of which have been found in Mexico (Shanks, 1977).

1. *Neolarra helianthi* Cockerell

This small parasitic bee was described by Cockerell (1936) from a male captured at *Helianthus petiolaris* in Colorado. Since the completion of this study, it has been placed as a synonym of the following species by Shanks (1977).

2. *Neolarra verbessinae* (Cockerell)

Recorded from flowers of *Helianthus* in Nebraska by Swenk (1907) and *H. petiolaris* in North Dakota by Stevens (1951a), this species ranges south to New Mexico, Arizona, and Texas according to Shanks (1977), who also records it from *Helianthus* sp. as well as other flowers. An additional *Helianthus* record was published for this species under the name *Neolarra helianthi* Cockerell (see above species account).

Genus *Holcopasites* Ashmead

Insofar as is known, the species of this North American genus are cleptoparasites in the nests of pollen-collecting bees belonging to the subfamily Panurginae of the family Andrenidae. Of the 15 species known, only the species treated below has been found at sunflowers.

3. *Holcopasites heliopsis* (Robertson)

This species, which ranges from Alberta, Montana, Colorado, and Illinois south to Arkansas and Kansas, has been recorded from *Helianthus* in Nebraska by Hurd and Linsley (1972). It may be a parasite of *Calliopsis nebraskensis* Crawford, which has not been found visiting *Helianthus*.

Genus *Epeolus* Latreille

Insofar as is known, the species of this chiefly Holarctic genus are cleptoparasitic in the nests of the genus *Colletes*. Of the 50 species known from America north of Mexico, only four have been taken at sunflowers.

4. *Epeolus autumnalis* Robertson

Robertson (1929) recorded the males as frequent at the flowers of *Helianthus divaricatus* in Carlinville, Illinois, and found both sexes visiting *H. tuberosus* at the same locality. It is believed that this species may be a parasite of *Colletes compactus*, an oligolege of Compositae secondarily associated with *Helianthus*.

5. *Epeolus bifasciatus* Cresson

Two subspecies are recognized: one, the nominate form, ranging from New England to Florida, west to Minnesota, Colorado, and Texas, and south into northern Mexico, has been collected by Robertson (1929) at *Helianthus divaricatus* (male only); the other, *E. b. obscuripes* Cockerell, ranges from Mexico to Panama and has not been taken at sunflower. *Epeolus bifasciatus* proper may be a parasite of *Colletes latitarsis* Robertson, which has not been taken at sunflowers.

6. *Epeolus compactus* Cresson

This species, which ranges from Illinois west to Texas, Colorado, Nevada, and California, has been reported at flowers of *Helianthus divaricatus* by Robertson (1898).

7. *Epeolus pusillus* Cresson

Robertson (1898, 1929) recorded a male of this species from flowers of *Helianthus divaricatus* in Illinois. It occurs from Maine to Florida and west to Texas and Wyoming. It is parasitic in the nests of several *Colletes* including those of *C. compactus*, an oligolege of the Compositae secondarily associated with *Helianthus*.

Genus *Triepeolus* Robertson

While most of the known host information suggests that these bees are cleptoparasites in the nests of eucerine bees (e.g., *Melissodes*, *Peponapis*, *Svastra*, and *Xenoglossa*), at least some species are known to be parasites of other Anthophoridae

(e.g., *Anthophora*, *Centris*) as well as Colletidae (*Ptiloglossa*), Oxaeidae (*Protoxaea*), and Halictidae (*Nomia*). The genus is almost exclusively New World in occurrence, with most of the species centered in North America, although a few species are present in South America and one of these ranges well northward into Central America. More than 100 species are found in America north of Mexico and 18 of these have been taken at the flowers of *Helianthus*. We have also collected a number of undescribed species from these flowers and anticipate that a great many more species of this genus will be found to visit sunflowers. Thus in the accounts that follow, only the described species are discussed.

8. *Triepeolus concavus* (Cresson)

FIGURE 7

This species, a parasite in the nest of *Svastra obliqua* (Custer, 1928, 1929b), is, like its host bee, a frequent visitor to *Helianthus*, from which both sexes extract nectar. Robertson (1922, 1929) designates it as one of the most regular visitors to sunflowers at Carlinville, Illinois, where he found it at seven local species of *Helianthus*: *H. annuus* (♂, ♀), *H. divaricatus* (♂, ♀), *H. grosseserratus* (♀ frequent), *H. mollis* (♀), *H. rigidus* (♂, ♀), *H. strumosus* (♀) and *H. tuberosus* (♀). Cockerell (1923) recorded it from *H. annuus lenticularis* at Oxford and Friend, Nebraska. The species ranges from North Carolina and Florida west to Illinois, Wisconsin, Colorado, and California.

Records of the collection of this species at principal sampling sites are presented in Tables K and M. Additional records are as follows:

ARIZONA.—GRAHAM COUNTY, Franklin, 6 Aug 75, *H. annuus*, 1130–1159, 1♂ (EGL, JML). YUMA COUNTY: Tacna, 29 July 75, *H. annuus*, 1415–1429, 1♂ (AEM, MMM); Wellton, 5 Sep 74, *H. annuus* 1100–1120, 1♀ (AEM, MMM).

CALIFORNIA.—RIVERSIDE COUNTY: Blythe, 29 Jun 74, *H. annuus*, 0800–0829, 1♂ (AEM, MMM). SAN JOAQUIN COUNTY: Victoria Island 0.5 mi E of Old River, 21 Jul 77, *H. annuus* (commercial sunflowers), 0930–0959, 3♂, at nest site of *Svastra obliqua* at edge of field of commercial sunflower, 1♀ (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Patterson, 27 Jul 77, 0930–0959, 2♂ (EGL, JML, AEM, MMM).

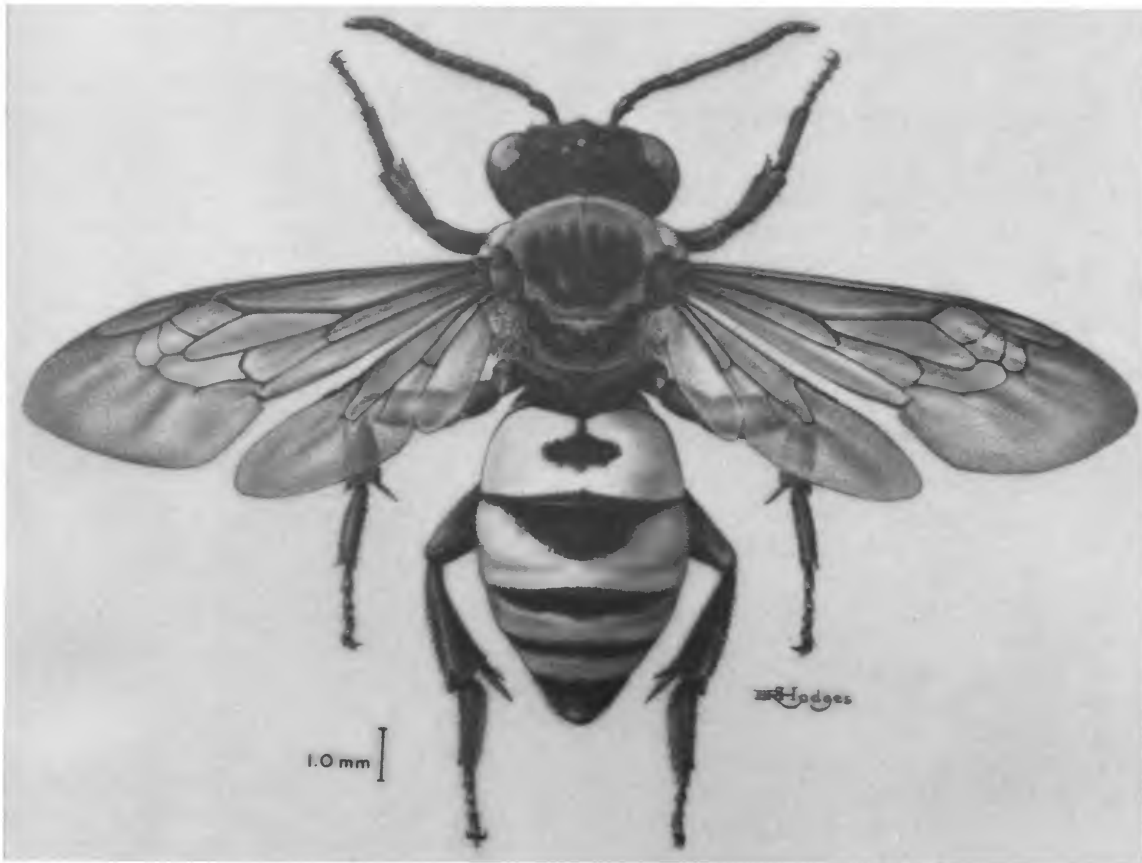


FIGURE 7.—*Triepeolus concavus* (Cresson), female. (Drawn by Elaine R. Hodges, Department of Entomology, Smithsonian Institution.)

At all the sites recorded above, *T. concavus* was visiting *H. annuus* in the company of *Svastra obliqua*.

9. *Triepeolus cressonii cressonii* (Robertson)

Robertson (1922) reported that this subspecies was one of the most regular visitors to *Helianthus* at Carlinville, Illinois, where he found it visiting five of the eight local species, including *H. divaricatus* (♂, ♀, frequent), *H. grosseserratus* (♀, frequent), *H. mollis* (♀), and *H. strumosus* (♂) (Robertson, 1929). It ranges from the New England states to North Carolina, Tennessee, and Minnesota.

Floral information is unavailable concerning

the other subspecies, *T. c. fraseri* Cockerell, described from New Mexico.

10. *Triepeolus cyclurus* Cockerell

Described originally from a female taken at flowers of *Helianthus petiolaris* near Wiggins, Colorado (Cockerell, 1923), no additional material has come to our attention.

11. *Triepeolus dacotensis* (Stevens)

A male and female have been recorded from flowers of *Helianthus petiolaris* in North Dakota by

Stevens (1919, 1951a). The species is also known from Utah.

12. *Triepeolus donatus* (Smith)

Triepeolus donatus has been reported at flowers of *Helianthus divaricatus* (♂, ♀, frequent) and *H. grosseserratus* (♂, ♀) by Robertson (1929), from *H. strumosus* (♀) by Graenicher (1909), and *H. sp.* by Mitchell (1962). It occurs from the New England states and southern Canada to Wisconsin and Georgia.

13. *Triepeolus helianthi* (Robertson)

The typical subspecies has been recorded from flowers of *Helianthus* by Robertson (1898) and Mitchell (1962), and more specifically from *H. grosseserratus* (♂, ♀, abundant) by Robertson (1929). Several subspecies have been recognized but their status needs review in the light of subsequent material. Collectively these occur from Wisconsin and Illinois to Colorado, New Mexico, and Arizona. The host of the nominate subspecies is *Melissodes (Eumelissodes) trinodis* (Graenicher, 1905) an oligoledge of Compositae, primarily associated with *Helianthus*. Hurd and Linsley (1959) present information that suggests that this species is also parasitic in the nests of *M. (Callimelissodes) composita*, an oligoledge of Compositae, secondarily associated with *Helianthus*. Robertson (1929) has recorded it in Illinois from *Helianthus divaricatus* and so does Pearson (1933).

14. *Triepeolus lestes* Cockerell

Known from Colorado and California, this species has been recorded from flowers of *Helianthus annuus* in Riverside County, California, by Moldenke and Neff (1974).

The capture of this species at sunflower in a principal survey site is reported in Table F. In addition, it was taken in another sample as follows:

CALIFORNIA.—INYO COUNTY: Tuttle Creek, 4 mi W of

Lone Pine, 29 Aug 77, *H. annuus*, 1030–1059, 1♂, 1♀ (EGL, JML).

At the sites where this species was taken, it was visiting the flowers in the company of *Melissodes agilis*.

15. *Triepeolus lineatulus* Cockerell and Sandhouse

Triepeolus lineatulus is a southwestern species, presently known from California and Arizona. In California it has been recorded at flowers of *Helianthus annuus*, *H. bolanderi*, and *H. sp.* by Moldenke and Neff (1974). Our collections of this species were made at two of the principal collecting sites (Tables H and K).

16. *Triepeolus lunatus* (Say)

This species has been recorded from *Helianthus divaricatus* (♂, ♀, frequent) and *H. tuberosus* (♀) in Illinois by Robertson (1898, 1929). Mitchell (1962) recognizes two subspecies, *T. lunatus lunatus* and *T. lunatus concolor*, both of which appear to have similar geographical ranges and both of which have been taken on *Helianthus* as well as other hosts. The species has been demonstrated to be a parasite of *Melissodes (Melissodes) bimaculata bimaculata*, which is a regular polyledge of *Helianthus*.

17. *Triepeolus nevadensis* (Cresson)

Robertson (1898, 1929) reported this species at flowers of *Helianthus divaricatus* (♀) in Illinois. It ranges from North Carolina and Georgia west to Nebraska, Nevada, and New Mexico.

18. *Triepeolus norae* Cockerell

We have been unable to find any prior flower records for this parasitic bee, which occurs in New Mexico and southern Arizona. We found this species in numbers at only one of our primary sampling sites (Table C).

19. *Triepeolus pectoralis* (Robertson)

Graenicher (1909) found females of this species visiting the flowers of *Helianthus strumosus* in Wisconsin. *Triepeolus pectoralis* ranges from Maine to Georgia and west to Minnesota, Colorado, and Utah. *Melissodes* (*Eumelissodes*) *rustica*, suspected of being one of its hosts, is an oligolege of the Compositae, secondarily associated with *Helianthus*.

20. *Triepeolus rectangularis* Cockerell

Triepeolus rectangularis is a western species (Colorado, Utah, Oregon, and California) that has been recorded as visiting flowers of *Helianthus* in California by Moldenke and Neff (1974).

21. *Triepeolus remigatus* (Fabricius)

This species has been recorded from *Helianthus* at Clarendon, Texas (Cockerell, 1914b), from *H. annuus lenticularis* at Friend, Nebraska (Cockerell, 1923), and *H. divaricatus* (♂) in Illinois by Robertson (1929). It is a widespread species ranging from New Jersey to Florida, west to Minnesota, Colorado, and California, and south to Texas, New Mexico, Arizona, and northern Mexico.

22. *Triepeolus simplex* Robertson

Recorded from *Helianthus divaricatus* (♀) in Illinois by Robertson (1929) and from the same plant near Chicago by Pearson (1933), this species ranges from Wisconsin, Illinois, and Michigan south to North Carolina and Georgia.

23. *Triepeolus subnitens* Cockerell and Timberlake

This species was described from a female captured at *Helianthus annuus*, at Riverside, California, in June.

We collected a single specimen in our surveys as follows:

CALIFORNIA.—SAN JOAQUIN COUNTY: Victoria Island 0.5 mi E of Old River, 21 Aug 77, entering burrow of *Suastra*

obliqua on edge of commercial sunflower field, 0930–0959, 1♀ (EGL, JML, AEM, MMM).

The presumed host, *S. obliqua*, is an oligolege of the Compositae primarily associated with *Helianthus*.

24. *Triepeolus texanus* (Cresson)

Cockerell (1898a) has recorded the male of *Triepeolus texanus* var. *nigripes* from flowers of *Helianthus ciliaris* from Mesilla, New Mexico. Currently this is regarded as a subspecies of *T. texanus*, the nominate subspecies is known only from Texas.

25. *Triepeolus trichopygus* Cockerell and Timberlake

This species was described from Riverside, California. Females were taken at *Senecio douglasii*, a male at *Gutierrezia sarothrae*. It was taken at one of our principal survey sites in New Mexico (Table C) visiting sunflowers.

Genus *Nomada* Scopoli

The bees of this genus are wasp-like in appearance and are present on all continents and many of the islands. They are cleptoparasites in the nests of other bees, principally those of the genus *Andrena*, but are also known to parasitize the nests of certain Halictidae, Melittidae, and Anthophoridae. As with many cleptoparasitic bees, they are often encountered either flying about the nesting sites of their hosts or sipping nectar with them at the same flowers.

The genus is represented in the Nearctic Region by nearly 300 species, of which seven have been taken at sunflowers. In addition to those discussed below, females of unidentified species of the subgenus *Micronomada* were taken at two localities in New Mexico (Animas and Rodeo) visiting flowers of *Helianthus annuus* in early September (EGL, JML).

**26. *Nomada (Heminomada) graenicheri*
Cockerell**

Graenicher (1909) found this species visiting flowers of *Helianthus giganteus* (♂) and *H. strumosus* (♂, ♀) in Wisconsin. This is the only locality known for the species.

27. *Nomada (Pachynomada) vincta vincta* Say

Both sexes of the nominate subspecies were recorded from *Helianthus* in Illinois by Robertson (1894) and Pearson (1933). In 1929, Robertson more specifically listed *H. grosseserratus* (♂, ♀, frequent) and *H. tuberosus* (♀). In Wisconsin, Graenicher (1909) found males at *H. strumosus*. This subspecies is widespread east of the Rocky Mountains and has been reported at flowers of other Compositae (*Grindelia*, *Solidago*, *Rudbeckia*, and *Aster*).

**28. *Nomada (Micronomada) garciana*
Cockerell**

Recorded by Cockerell (1914b) from *Helianthus* at Falfurrias, Texas, this species is known only from New Mexico and Texas.

**29. *Nomada (Micronomada) gutierreziae*
Cockerell**

The type specimen was taken on *Gutierrezia* in Mesilla Valley, New Mexico. The species is also known from Colorado and Arizona.

Examples were taken at sunflowers as follows:

ARIZONA.—SANTA CRUZ COUNTY: Patagonia, 5 Sep 75, *H. annuus*, 0900–1000, 3♂, 10♀ (EGL, JML).

**30. *Nomada (Micronomada) melanoptera*
Cockerell**

Stevens (1951a) reported this species at flowers of *Helianthus petiolaris* in North Dakota. The species was described from Colorado and is known only from these two states.

31. *Nomada (Micronomada) texana* Cresson

This species ranges from Massachusetts south to North Carolina and Alabama and west to Michigan, Colorado, and Arizona. Cockerell (1914b) recorded the species at *Helianthus* in Falfurrias, Texas, and Mitchell (1962) included this host among his flower records.

32. *Nomada (Micronomada) vierecki* Cockerell

Recorded from *Helianthus petiolaris* in North Dakota (Stevens, 1951a), this species also occurs in Nebraska, Colorado, New Mexico, Texas, and Mexico.

Genus *Paranomada* Linsley and Michener

The species of this genus are found only in the southwestern United States and adjacent northern Mexico (Arizona, California, and Baja California). They are parasites in the nests of *Exomalopsis*. One of the three known species has been taken at flowers of *Helianthus*.

33. *Paranomada velutina* Linsley

This parasitic bee has not been recorded previously from *Helianthus*, but a single example was collected during our primary surveys (Table C). Previously the species was known only from Arizona and Baja California, but is now known to occur in New Mexico. Rozen (1977) has recently established that this species is a parasite in the nests of *Exomalopsis solani*, which is a casual polylege of *Helianthus*.

Genus *Exomalopsis* Spinola

Although primarily a genus of Neotropical bees, 31 species are present in America north of Mexico and four of these have been found to visit sunflowers. Three are casual polyleges and *Exomalopsis pygmaea* is an oligolege of the Compositae, primarily associated with *Helianthus*.

**34. *Exomalopsis (Phanomalopsis) solani*
Cockerell**

Exomalopsis solani ranges from Texas to Colorado and Arizona and south into Mexico. Timberlake (1947) gives a wide range of flower records for this species but apparently it has not been recorded previously from *Helianthus*. Females, including some pollen collectors, were taken at primary study sites in New Mexico and Arizona (Tables C and D). It appears to be a casual polylege of *Helianthus*.

**35. *Exomalopsis (Phanomalopsis) solidaginis*
Cockerell**

This species is related to *E. solani* but is generally smaller and differs in several structural characters. It visits many Compositae, including *Helianthus*, and ranges from Texas to southern California and south into Mexico. It appears to be a casual polylege of *Helianthus*.

One example of this species was taken at a principal sampling site (Table C). In addition, specimens were taken at sunflowers as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0829, 2♂, 1♀N (EGL, JML). SANTA CRUZ COUNTY: Sonoita, 16 Sep 74, *H. annuus*, 1♀N (PDH, AEM, MMM).

**36. *Exomalopsis (Anthophorisca) morgani*
Cockerell**

This species was described originally from a female taken on flowers of *Helianthus* at Falfurrias, Texas (Cockerell, 1914a). The species ranges from Texas to southern Arizona and southward to Oaxaca, Mexico. It evidently is a casual polylege of *Helianthus*.

**37. *Exomalopsis (Anthophorisca) pygmaea*
(Cresson)**

Records of this species from *Helianthus* have largely been reported under the name "*bruneri*." Thus, Crawford (1902) reported the species from *H. annuus* at Lincoln, Nebraska, Cockerell (1911) from *H. lenticularis* at Sterling, Colorado, where

both sexes were common on the flowers, and from *H. sp.* at Dallas, Texas (Cockerell, 1914a).

Timberlake (in litt.) in his review of the genus, examined 262 specimens from Kansas, mainly from Lawrence and vicinity and mostly from flowers of *Helianthus*. In addition he listed the following records:

ARIZONA.—COCHISE COUNTY: 1.5 mi W of Saint David, 9 Sep 61, *H. annuus*, 6♂ (P. D. Hurd, Jr.).

COLORADO.—LOGAN COUNTY: Sterling, 3 Aug 11, *H. lenticularis*, 1♂, 3♀ (T.D.A. Cockerell).

TEXAS.—BEXAR COUNTY: 22 Jun 63, on *Helianthus*, 1♂ (A. H. Alex). BRAZOS COUNTY: 13 Oct 54, on *Aster*, 1♀ (A. H. Alex). DALLAS COUNTY: Dallas, 22 Sep 05, on *Helianthus*, 2♂ (F. C. Bishop). KARNES COUNTY: Range, 24 Sep 04, on *Helianthus*, 1♀ (J. C. Crawford). TRAVIS COUNTY: 10 mi SE of Austin, 27 Sep 65, on *Chrysopsis viscida*, 1♀ (G. E. Bohart).

The species is an oligolege of the Compositae, primarily associated with *Helianthus*.

Genus *Ptilothrix* Smith

This is a Neotropical genus that occurs on both the North and South American continents and contains relatively few species. Only two of these are known to occur in America north of Mexico and only the one treated below is known to visit sunflowers.

38. *Ptilothrix* sp. near *sumichrasti* Cresson

This species was recorded as *P. sumichrasti* from *Kallstroemia grandiflora* by Cazier and Linsley (1974); however, although closely related it is apparently an undescribed species. We record the following collection of this *Ptilothrix* sp.:

ARIZONA.—PIMA COUNTY: 6 mi W of Rillito, 12 Aug 75, *H. annuus*, 0930-0959, 1♂ (EGL, JML).

Genus *Diadasia* Patton

Bees of this genus occur only in the Americas and are distributed chiefly in the warm temperate areas of North and South America, although a few species are present in the moist tropics. Most, if not at all, species are oligolectic, obtaining pollen primarily from the Malvaceae (*Callirhoe*,

Sida, *Sidalcea*, and *Sphaeralcea*), Convolvulaceae (*Calystegia*, *Convolvulus*), Compositae (*Helianthus*), Cactaceae (*Opuntia*), and the Onagraceae (*Clarkia*). Twenty-five species are currently recognized from America north of Mexico and seven of these have been taken from sunflowers. Of these, all are nectar visitors except *Diadasia enavata*, which is an oligolege of the Compositae, primarily associated with *Helianthus*.

39. *Diadasia afflicta afflicta* (Cresson)

A female was recorded from *Helianthus* at Falfurrias, Texas, by Cockerell (1914b). She carried only a little pollen on the legs, both cactaceous and from sunflower and had *Helianthus* grains on the wings. This subspecies occurs in Texas and New Mexico and collects pollen normally from flowers of *Callirhoe* and presumably visit *Helianthus* for nectar only.

40. *Diadasia australis* (Cresson)

Cockerell (1914b) reported a female of *D. australis australis*, an oligolege of Cactaceae, at *Helianthus* at Falfurrias, Texas. She had collected much yellow pollen on the legs. The large smooth grains were apparently cactaceous, but there were small grains of *Helianthus* scattered about. Males of the far western subspecies, *D. australis californica* Timberlake, have been recorded from sunflower at San Bernardino, California, by Viereck (1902) and Cockerell (1914b), and from *Helianthus gracilentus* at The Gavilan, Riverside County, California, by Timberlake (1940).

The species, which occurs from Texas to California and Colorado and also is present in Mexico, appears to visit *Helianthus* for nectar.

41. *Diadasia bituberculata* (Cresson)

Diadasia bituberculata is an oligolege of Convolvulaceae in California. The male occasionally visits sunflower for nectar. We record:

CALIFORNIA.—LOS ANGELES COUNTY: Tujunga Canyon, Sunland, 14 May 75, *H. annuus*, 1245-1259, 1♂ (AEM, MMM).

42. *Diadasia diminuta* (Cresson)

This species, which ranges from British Columbia to California and east to Nebraska, Kansas, and Texas, was formerly believed to be an oligolege of *Opuntia*. Cazier and Linsley (1974) found females taking pollen from *Kallstroemia grandiflora*. It occasionally visits sunflower for nectar.

One male of this species was taken at sunflower in a principal survey site (Table D). In addition, a single collection was made as follows:

CALIFORNIA.—SAN DIEGO COUNTY: Vicinity of Laguna Junction on Highway 8, 13 Jul 74, *H. petiolaris*, 1300-1415, 1♂ (AEM, MMM).

43. *Diadasia enavata* (Cresson)

FIGURE 8; PLATE 2

Diadasia enavata is an oligolege of Compositae, primarily *Helianthus* (Linsley and MacSwain, 1957, 1958). Females have been reported at flowers of *Helianthus* sp. at Fedor, Texas (Cockerell, 1906a), *H. annuus* (later recorded as *H. lenticularis*, 1914b) at Mesilla, New Mexico (Cockerell, 1905), at Delta, Utah (Bohart, et al., 1950), and in Fresno County, California (Moldenke and Neff, 1974), *H. lenticularis* at Orange, California (Cockerell, 1916a), and *H. gracilentus* in Riverside County, California (Moldenke and Neff, 1974). The nest architecture has been figured by Bohart (1952) and described and illustrated by Linsley and MacSwain (1957). It is characterized by a long, erect entrance turret, a long vertical shaft (approximately 13 cm), branching at the bottom of the shaft to provide for numerous cells (14-42) many of which are arranged in semivertical series. In California, the species is parasitized by larvae of the bombyliid, *Anthrax nidicola* Cole. At Delta, Utah, Bohart et al. (1950) found the females nesting gregariously in dry, hard-packed, sandy soil; near Pittsburg, Contra Costa County, California, Linsley and MacSwain (1957), found them nesting in well-separated burrows associated with grass in a flat pastureland.

As a species, *D. enavata* has a long flight season, suggesting more than one annual generation. In the San Joaquin Valley of California, both sexes

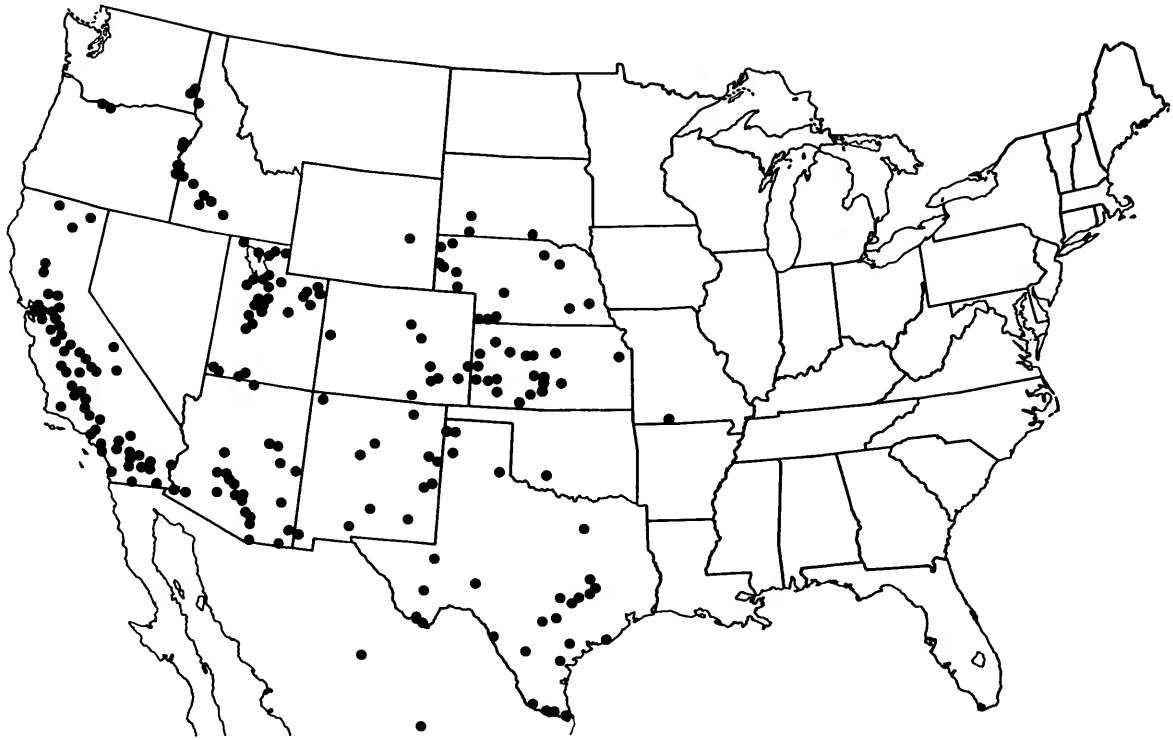


FIGURE 8.—Distribution of *Diadasia enavata* (Cresson).

have been collected from June to October. On 6 October 1975, between 0800 and 1400 hrs at Corcoran, Kings County California, 319 freshly emerged males, representing nearly 50 percent of all the bees present (the total including only eight females), were visiting the flowers of *H. annuus*. Males also sleep on the flower heads, usually, but not always, singly.

Diadasia enavata was present at most of the sunflower sites sampled except those in the Chihuahuan desert areas of southeastern Arizona and western New Mexico. Adlakha (1969), however, cites localities in this region. The only female of this species collected in this area is recorded as follows:

NEW MEXICO.—HIDALGO COUNTY: 1 mi SW of Rodeo, 15 Aug 72, *H. annuus*, 1110–1140, 1♀P (T. J. Zavortink).

Adlakha (1969) lists as nectar sources for one or both sexes of *D. enavata*, species in two genera

of Capparidaceae, 13 genera of Compositae, one genus each of Cruciferae and Cucurbitaceae, three of Leguminosae, and one each of Scrophulariaceae and Verbenaceae. Of the pollen-bearing females examined by him, 143 were from *Helianthus*, 21 from *Grindelia*, and three from *Coreopsis lanceolata*. He states, however, that the species is restricted to Compositae, the preferred genera being *Helianthus*, *Grindelia*, and *Centaurea* in the order given, although he lists only 10 males and a nectar-seeking female from the latter genus.

This is the most wide-ranging species of the genus in America north of Mexico. It ranges from Washington south to California and into Mexico and east to South Dakota, Nebraska, Missouri, Oklahoma, and Texas. It is the only North American species of the genus oligolectic on composites and has a finely plumose scopa well adapted to carry the fine pollen grains of these plants.

Diadasia enavata was represented in most of our

principal surveys (Tables G-M) in California. Additional samples were taken as follows:

ARIZONA.—MARICOPA COUNTY: Theba, 28 Jun 74, *H. annuus*, 0955–1005, 16♂, 1130–1159, 38♂, 2♀N (AEM, MMM). PIMA COUNTY: Marana, 30 Jul 75, *H. annuus*, 1100–1114, 2♂ (AEM, MMM); Rillito, 6 mi W, 27 Jun 74, *H. annuus*, 0830–0929, 8♀P (AEM, MMM), 30 Jul 75, *H. annuus*, 1345–1514, 29♂, 23♀P, 19♀N (EGL, JML, AEM, MMM), 12 Aug 75, *H. annuus*, 0930–1059, 28♂, 6♀P, 10♀N (EGL, JML); Sahuarita, 15 Jun 74, *H. annuus*, 1200–1229, 6♂, 2♀P, 1♀N (AEM, MMM). PINAL COUNTY: Eloy, 14 Jun 74, *H. annuus*, 1130–1259, 55♂, 17♀P, 24♀N (AEM, MMM), 26 Jun 74, *H. annuus*, 0630–0659, 2♂ (AEM, MMM), 30 Jul 75, *H. annuus*, 0815–0929, 7♂, 13♀P, 12♀N (AEM, MMM); Stanfield, 30 Jul 75, *H. annuus*, 0730, 1♂ (AEM, MMM). YUMA COUNTY: Tacna, 29 Jul 75, *H. annuus*, 1415–1429, 2♂ (AEM, MMM); Wellton, 5 Oct 74, *H. annuus*, 1100–1129, 9♂ (AEM, MMM).

CALIFORNIA.—CONTRA COSTA COUNTY: Byron 4 mi E, 21 Jul 77, *H. annuus*, 0800–0829, 1♂, 1♀P (EGL, JML, AEM, MMM). FRESNO COUNTY: Coalinga 10 mi N, junction with Highway 5, 10 Sep 75, *H. annuus*, 1115–1144, 10♂, 3♀P (AEM, MMM); Parlier, 7 Sep 75, *H. annuus*, 1400–1429, 2♂ (EGL, JML, AEM, MMM). IMPERIAL COUNTY: El Centro, 29 Jul 75, *H. annuus*, 1000–1029, 13♂, 7♀P, 1♀N (AEM, MMM). KERN COUNTY: Bakersfield 8 mi S on Highway 99, 22 Aug 76, *H. annuus*, 1030–1059, 1♂, 1♀N (AEM, MMM); Junction Highway 5 with 99, *H. annuus*, 1230–1259, 14♂, 6♀P, 6♀N (AEM, MMM); Highway 5 at Old River Road, 10 Sep 75, *H. annuus*, 1400–1415, 5♂ (AEM, MMM); Highway 5, 3 mi S Lost Hills, Paso Robles Junction with Highway 46, 29 Jul 76, *H. annuus*, 1100–1129, 2♀P (AEM, MMM); Copus Road between Highway 5 and 99, *H. annuus*, 1130–1159, 35♂, 12♀ (AEM, MMM), 1430–1445, 7♂, 2♀P, 1♀N (AEM, MMM); Metler, 23 Sep 76, *H. annuus*, 1200, 4♂ (AEM, MMM); Wheeler Ridge, 23 Sep 76, *H. annuus*, 1245, 3♀P (AEM, MMM). LOS ANGELES COUNTY: Gorman, 29 Aug 76, *H. annuus*, 0800–0829, 2♀P (AEM, MMM). MERCED COUNTY: Atwater, 23 Jul 77, *H. annuus*, 1100–1129, 2♂, 21♀P, 4♀N (EGL, JML, AEM, MMM). RIVERSIDE COUNTY: Blythe, 29 Jun 74, *H. annuus*, 0800–0829, 4♂ (AEM, MMM); Coachella, 8 Jun 76, *H. annuus*, 0800–0829, 32♂, 1♀P, 1♀N (EGL, JML); Indio, 8 Jun 76, *H. annuus*, 0700–0829, 47♂, 1400–1429, 20♂ (EGL, JML). SAN JOAQUIN COUNTY: Manteca, 7.5 mi N, 21 Jul 77, *H. annuus*, 1100–1129, 4♂, 2♀P (AEM, MMM). STANISLAUS COUNTY: Grayson 6.5 mi N, 27 Jul 77, *H. annuus*, 1100–1129, 38♂, 4♀P (EGL, JML, AEM, MMM); Modesto, 3 Oct 75, *H. annuus*, 0745–0759, 2♂ (EGL, JML); Modesto 10 mi S, 27 Jul 77, *H. annuus*, 0800–0829, 1♂, 46♀P (EGL, JML, MMM); Patterson, 27 Jul 77, *H. annuus*, 0930–0959, 2♂, 1♀P (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Sep 75, *H. annuus*, 1530, 2♂ (EGL, JML, AEM, MMM); Tulare, 6 Sep 75, *H. annuus*, 1600–1629, 1♂ (EGL, JML, AEM, MMM).

TEXAS.—TRAVIS COUNTY: Austin, 12–18 Sep 78, *H. annuus*, 79♂, 183♀P, 9♀N (PDH).

44. *Diadasia ochracea* (Cockerell)

This species ranges along the Pacific Coast states from Washington to southern California, west to Texas, and south into Mexico. At one time thought to be an oligolege of *Sphaeralcea* (Linsley and MacSwain, 1957) it was reported taking pollen from *Kallstroemia grandiflora* by Cazier and Linsley (1974). Both sexes occasionally visit *Helianthus* for nectar. A few specimens of this species were taken at the principal study sites (Tables B, C).

45. *Diadasia rinconis rinconis* Cockerell

This species ranges from Texas to southern California and south into Mexico (Baja California). The females collect pollen from *Opuntia*, but both sexes visit other flowers for nectar including *Helianthus*.

Specimens have been taken at sampling sites as follows:

ARIZONA.—PIMA COUNTY: Rillito, 5 mi W, 30 Jul 75, *H. annuus*, 1330–1344, 1♂ (AEM, MMM); Sahuarita, 15 Jul 74, *H. annuus*, 5♂, 6♀N, 26 Jun 74, *H. annuus*, 4♂, 4♀N (AEM, MMM).

Genus *Synhalonia* Patton

The bees of this North American genus fly primarily during the spring months and are observed only exceptionally during the summer. A second generation may occur in some species since specimens have been taken as late as August. Usually, the females do not collect pollen from flowers of Compositae, but visit the flowers of a wide range of plant families, including especially the Ranunculaceae, Leguminosae, Hydrophyllaceae, Boraginaceae, and Saxifragaceae (Timberlake, 1969b).

More than 50 species are known from America north of Mexico and only two of these visit sunflowers and possibly may be casual polyleges of those plants.

46. *Synhalonia actiosa* (Cresson)

Recorded by Timberlake (1969b) from a long list of flower genera, including *Helianthus nuttallii*, this species is polylectic and ranges from Washington and Idaho south to California, Utah, Arizona, and New Mexico. It may be a casual polylege of *Helianthus*.

47. *Synhalonia edwardsii* (Cresson)

This is a western North American species ranging from British Columbia to Montana and southward to New Mexico, Arizona, California, and Baja California Norte. It is highly polylectic. Timberlake (1969b) includes *Helianthus* among the wide range of flowers visited. The species may be a casual polylege of *Helianthus*.

Genus *Syntrichalonia* LaBerge

This is a monotypic genus found only in the southwestern United States and adjacent Mexico as far south as the state of Jalisco and the Federal District.

48. *Syntrichalonia exquisita* (Cresson)

This elegant species ranges from Texas to Arizona and south into Mexico (D. F., Durango, Jalisco, and Zacatecas).

Zavortink (1975) comments on this species as follows:

In southeastern Arizona, *exquisita* occurs most commonly in montane, forested regions, where it visits the flower heads of several species of Compositae for both nectar and pollen during the warmest part of the day in the late summer and early fall. All my records of this species are from composites with large, showy, yellow, radiate heads in the related predominantly American tribes Helenieae and Heliantheae, namely: *Helenium hoopesii* Gray, *Helianthus annuus* L., *Heliopsis parvifolia* Gray, *Verbesina encelioides* (Cav.) Benth. & Hook., and *Viguiera dentata* (Cav.) Spreng. Other specimens of *exquisita* that I have examined were collected on *Asclepias* sp. (Asclepiadaceae), *Chrysopsis* sp. (Compositae, Astereae), *Encelia* sp. (Compositae, Heliantheae), *Helianthus annuus*, and *Verbesina oreophila* Woot. & Standl.

At Rucker Canyon, Chiricahua Mountains, in 1974, *exquisita* was active between 0930 and 1615 MST (Table 3).

The air temperature in the upper, narrow part of the canyon, where *exquisita* visited flowers of *Viguiera dentata*, varied from 20–24° C during this time interval; the air temperature in the lower, broad part of the canyon, where it visited *Verbesina encelioides*, was 27° C at the time specimens were collected in the afternoon. At Rodeo, New Mexico, a male *exquisita* was collected from *Helianthus annuus* by E. G. and J. M. Linsley between 1630 and 1659 MST when the temperature was 34° C.

Females of *exquisita* alight on the disks of the composite heads and gather the fine pollen grains characteristic of these plants in their dense, highly plumose scopal hairs. Males fly rapidly around and over the flower-bearing plants and alight occasionally to drink nectar. The foraging of females and the patrolling of males continue, but at reduced levels, when the sun is obscured by clouds for either short or long intervals.

The seasonal flight period of *exquisita* in southwestern United States is during and after the summer rainy season. The earliest and latest collection dates are 10 August and 4 October, and the greatest number of specimens has been collected in September. The seasonal flight period in Mexico is known to extend from 27 July to December

It is thus an oligolege of the Compositae, secondarily associated with *Helianthus*.

Pollen-collecting records for this species at sunflowers are listed in Tables A and C. In addition, it was captured at an additional site as follows:

ARIZONA.—SANTA CRUZ COUNTY: Nogales, 17 Sep 74, *H. annuus*, 1♀N (PDH, AEM, MMM).

Genus *Svastra* Holmberg

The bees of this genus are found only in the Western Hemisphere. The nominate subgenus is represented by three species in South America (Argentina and Chile) and two subgenera (*Brachymelissodes* and *Epimelissodes*), which include about 15 species from North and Central America. Most of these (14 species) occur in America north of Mexico and the majority of these (11) have been taken at sunflowers. Six of these are oligoleges of Compositae either primarily (3 species) or secondarily (3 species) associated with *Helianthus*. The remaining species (5) are either casual polyleges (2) or nectar seekers (3).

These are among the larger-sized bees found at sunflowers and are, as a group, exceptionally valuable pollinators of this plant.

49. *Svastra (Brachymelissodes) cressonii* (Dalla Torre)

This apparently polylectic bee has been recorded from *Helianthus annuus* by LaBerge (1956a). The species ranges from Iowa, Nebraska, and eastern Colorado through Kansas and western Oklahoma to Durango, Mexico. It is known to collect pollen from the flowers of *Euphorbia marginata* and also possibly *Vernonia*. It may be a casual polylege of *Helianthus*.

50. *Svastra (Epimelissodes) aegis* (LaBerge)

Svastra (E.) aegis was recorded by LaBerge (1956a) and Mitchell (1962) from *Helianthus* and related Compositae, LaBerge specifically listing *H. annuus* and *H. radula*. The species ranges from North Carolina to Florida and Texas. It appears to be an oligolege of the Compositae secondarily associated with *Helianthus*.

51. *Svastra (Epimelissodes) atripes atripes* (Cresson)

LaBerge (1956a) includes *Helianthus annuus* among the flower records for this subspecies, which ranges from Illinois, Missouri, and Louisiana, west to New Mexico and Colorado. To judge from the available floral data, this subspecies is evidently a casual polylege of *Helianthus*.

52. *Svastra (Epimelissodes) grandissima* (Cockerell)

Svastra grandissima has not been recorded from *Helianthus* previously. The species is known from southeastern Texas and, with the new record cited below, Arizona. It has been taken on *Verbesina encelioides* and possibly visits *Helianthus* for nectar only.

Our only record of this species from sunflower is as follows:

ARIZONA.—YUMA COUNTY: Wellton, 28 Jun 74, *H. annuus*, 1400–1410, 1♂ (AEM, MMM).

53. *Svastra (Epimelissodes) helianthelli* (Cockerell)

This species occurs from western Texas and Kansas to southern California and northern Baja California. It was described originally from *Helianthus ciliaris* at Mesilla, New Mexico. LaBerge (1956a) recorded the capture of both sexes on *Helianthus* sp., and *H. ciliaris*. Subsequently he (LaBerge, 1958) provided additional Arizona records from *Helianthus* sp. and a southern California record from *H. annuus*. It appears from the available floral data to be an oligolege of the Compositae, primarily associated with *Helianthus*.

Details of the collection of this species from a principal survey site are to be found in Table C. Additional records from sampling sites are as follows:

ARIZONA.—MARICOPA COUNTY: Theba, 28 Jun 74, *H. annuus*, 0955–1159, 4♂ (AEM, MMM). PIMA COUNTY: Rillito, 6 mi W, 31 Jul 75, *H. annuus*, 0805, 1♀P, 1500–1515, 1♂ (EGL, JML, AEM, MMM). YUMA COUNTY: Tacna, 28 Jun 74, *H. annuus*, 1305–1325, 5♂ (AEM, MMM), 29 Jul 75, *H. annuus*, 1415–1429, 8♂ (AEM, MMM); Wellton, 28 Jun 74, *H. annuus*, 1100–1129, 6♂ (AEM, MMM); Yuma, 29 Jul 75, *H. annuus*, 1300–1314, 2♂ (AEM, MMM).

CALIFORNIA.—IMPERIAL COUNTY: El Centro, 29 Jul 75, *H. annuus*, 1000–1029, 5♂ (AEM, MMM).

54. *Svastra (Epimelissodes) machaerantherae* (Cockerell)

LaBerge (1956a) recorded both sexes of this species from *Helianthus* sp. and males from *H. annuus*. It ranges from Texas (El Paso) to southern California and south into northern Mexico. Males “sleep” in large, massed balls on the tallest dried flower stalks, gathering noisily at about sunset (observations at Rodeo, Hidalgo County, New Mexico, and near Apache, Cochise County, Arizona). During the day they patrol the flower heads continuously, at about the level of the tallest plants, pausing briefly for nectar from time to time.

The species is evidently an oligolege of the Compositae, primarily associated with *Helianthus*.

Details of the collections of this species at the

principal survey sites are presented in Tables A-D. Additional records are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830-0859, 1♂ (EGL, JML). PIMA COUNTY: San Xavier, 19 Sep 74, *H. annuus*, 1200-1229, 1♀P (PDH, AEM, MMM). SANTA CRUZ COUNTY: Sonoita, 16 Sep 74, *H. annuus*, 1♂, 2♀N (PDH, AEM, MMM).

CALIFORNIA.—RIVERSIDE COUNTY: Indio, 18 Sep 77, *H. annuus*, 0800-0829, 1♂ (EGL, JML).

55. *Svastra (Epimelissodes) obliqua* (Say)

FIGURE 9; PLATE 3

This widespread, variable species ranges from coast to coast in the United States and southern Canada and into northern Mexico. Graenicher (1909) recorded males from *Helianthus strumosus* and Robertson (1929) listed this species from *H.*

annuus (♂, ♀P), *H. divaricatus* (♂, ♀P, abundant), *H. grosseserratus* (♂, ♀P), *H. mollis* (♂, ♀P, frequent), *H. rigidus* (♂, ♀P), *H. strumosus* (♂, ♀P, frequent), and *H. tuberosus* (♀P, abundant). LaBerge (1956a) summarized flower records for 1128 individuals, of which 730 were females. Of these, all but 48 were from Compositae. He concluded that they prefer Heliantheae, Vernonicaceae, Astereae, and Helenieae in that order. Three subspecies are recognized by LaBerge: *S. obliqua caliginosa* (Cresson) occurring along the Atlantic coast states from New Jersey to Georgia; *S. obliqua obliqua* ranging from southern Ontario and eastern Montana, south to New Mexico and New Jersey and west of the Appalachians to Florida and Mexico (Tamaulipas and Coahuila); and *S. obliqua expurgata* (Cockerell) ranging from Washington and Idaho to northern Baja California, Arizona, and western

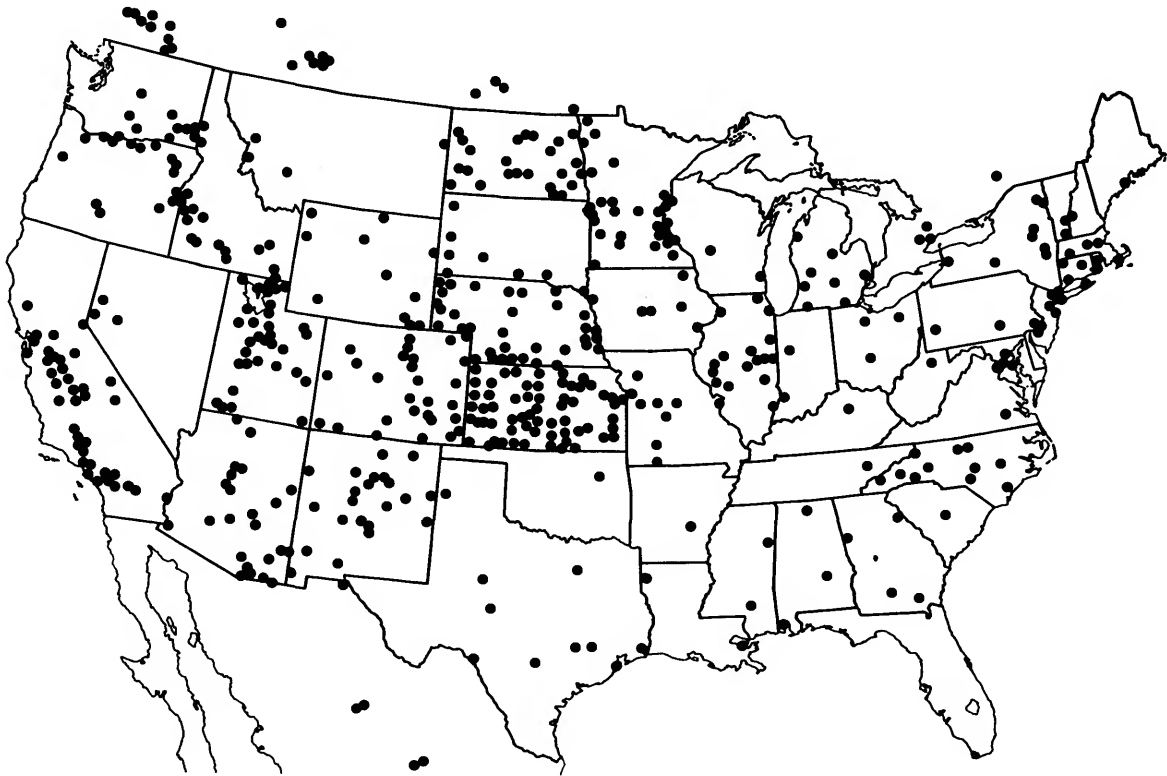


FIGURE 9.—Distribution of *Svastra (Epimelissodes) obliqua* (Say).

Colorado. *Svastra obliqua caliginosa* has been recorded from *Helianthus* sp., *H. atrorubens*, *H. microcephalus*, and *H. zonatus*; *S. obliqua* from *Helianthus* sp., *H. annuus*, *H. divaricatus*, *H. grosseserratus*, *H. laetiflorus*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. scaberrimus*, *H. strumosus*, and *H. tuberosus*; and *S. obliqua expurgata* from *Helianthus* sp., *H. annuus*, *H. bolanderi*, *H. ciliaris*, and *H. petiolaris*.

The nesting habits of this species have been described by Custer (1928) and Rozen (1964).

It, along with *Melissodes agilis*, is one of the most ubiquitous of sunflower bees. Males cruise the flower heads throughout the day, flying about the highest plants. *Svastra obliqua* is an oligolege of the Compositae, primarily associated with *Helianthus*.

Details of collections of the subspecies, *S. o. expurgata* at primary sampling sites may be found in Tables A-D and H-M. Additional collections are as follows:

ARIZONA.—MARICOPA COUNTY: Theba, 28 Jun 74, *H. annuus*, 0955-1159, 3♂ (AEM, MMM). PIMA COUNTY: Marana, 27 Jun 74, *H. annuus*, 1030-1059, 5♂, 2♀ (AEM, MMM), 30 Jul 75, *H. annuus*, 1100-1114, 1♀, 1♀ (AEM, MMM); Rillito 6 mi W, 27 Jun 74, *H. annuus*, 0830-0929, 1♂, 2♀, 1♀ (AEM, MMM), 31 Jul 75, *H. annuus*, 1500-1529, 1♂, 3♀ (EGL, JML, AEM, MMM), 12 Aug 75, *H. annuus*, 0930-1059, 1♂, 1♀ (EGL, JML). PINAL COUNTY: Eloy, 26 Jun 74, *H. annuus*, 0630-0659, 1♂, 1♀ (AEM, MMM), 30 Jul 75, *H. annuus*, 0815-0829, 1♂ (AEM, MMM). SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0800-0829, 1♂, 4♀ (EGL, JML); Sonoita 10 mi E, 7 Sep 77, *H. petiolaris*, 0830-0859, 1♂, 2♀ (EGL, JML). YUMA COUNTY: Tacna, 28 Jun 74, *H. annuus*, 1305-1325, 7♂ (AEM, MMM), 29 Jul 75, *H. annuus*, 1415-1429, 1♂ (AEM, MMM); Yuma, 29 Jul 75, *H. annuus*, 1300-1314, 2♀ (AEM, MMM).

CALIFORNIA.—FRESNO COUNTY: Parlier, 7 Oct 75, *H. annuus*, 1400-1429, 1♂, 5♀, 1♀ (EGL, JML, AEM, MMM); Selma, 6 Oct 75, *H. annuus*, 1030, 1♀ (EGL, JML, AEM, MMM). IMPERIAL COUNTY: Holtville 3 mi W, 29 Jul 75, *H. annuus*, 1100-1114, 1♂, 3♀, 3♀ (AEM, MMM). INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0800-0829, 1♀ (EGL, JML). KERN COUNTY: Bakersfield 8 mi S, 22 Aug 76, *H. annuus*, 1030-1059, 1♀, 1♀ (AEM, MMM); Copus Road between Highways 5 and 99, 22 Aug 76, *H. annuus*, 1130-1159, 1♂, 4♀ (AEM, MMM); Highway 5 junction with Highway 99, 22 Aug 76, *H. annuus*, 1230-1259, 1♂, 1♀ (AEM, MMM); Highway 5, 3 mi S of Lost Hills, Paso Robles Junction, 29 Jul 76, *H. annuus*, 1100-1129, 1♂, 12♀, 3♀ (AEM, MMM); Highway 99, Visalia-Hanford Junction, 22 Aug 76, *H. annuus*, 0730-0829, 17♀, 6♀ (AEM, MMM). MERCED COUNTY: Atwater, 23 Jul 77, *H. petiolaris*,

1200-1229, 1♂, 1♀ (EGL, JML, AEM, MMM). RIVERSIDE COUNTY: Blythe, 29 Jun 74, *H. annuus*, 0800-0829, 2♂, 1♀ (AEM, MMM), 5 Jun 77, *H. annuus*, 1200, 1♂ (EGL, JML). SAN JOAQUIN COUNTY: Manteca, 27 Jul 77, *H. annuus*, 1230-1259, 3♂ (EGL, JML, AEM, MMM); Manteca 7.5 mi N, 27 Jul 77, *H. annuus*, 1100-1129, 4♂ (EGL, JML); Victoria Island 0.5 mi E of Old River, 21 Jul 77, *H. annuus* (commercial field), 0930-0959, 2♂, 1♀, 1♀ (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Grayson 6.5 mi N, 27 Jul 77, *H. annuus*, 1100-1129, 1♂ (EGL, JML, AEM, MMM); Modesto 10 mi S, 27 Jul 77, *H. annuus*, 0800-0829, 1♀ (EGL, JML, AEM, MMM); Patterson, 27 Jul 77, *H. annuus*, 0930-0959, 27♂, 6♀ (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Sep 75, *H. annuus*, 1200-1230, 2♂, 3♀ (EGL, JML, AEM, MMM).

56. *Svastra (Epimelissodes) petulca* (Cresson)

Two subspecies are recognized by LaBerge (1956a), *S. (E.) petulca petulca* (Cresson), ranging from eastern Texas north through Kansas to Illinois, east to Florida, and north along coast to New Jersey. He records it from *Helianthus* sp. and other composites. The other subspecies, *S. (E.) petulca suffusa* (Cresson), occurs from northeastern Kansas and eastern Colorado to Texas, New Mexico, and northern Arizona and is reported from *Helianthus* sp., *H. annuus*, and other flowers, mostly Compositae. The species appears to be an oligolege of Compositae, secondarily associated with *Helianthus*.

For records of *Svastra petulca suffusa*, see Table C. An additional specimen was taken as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830-0859, 1♀ (EGL, JML).

57. *Svastra (Epimelissodes) sabinensis* (Cockerell)

LaBerge (1956a) recognizes three subspecies of *S. sabinensis*: *S. s. nubila* (LaBerge) from southern California and Baja California, *S. s. sabinensis* from southern California to New Mexico, and *S. s. laterufa* (Cockerell) from New Mexico and Texas to Mexico. The male holotype of the subspecies *nubila* was collected on *Helianthus annuus* at Riverside, California, on 8 July 1927. Practically all examples collected subsequently have been males at various species of Compositae, in particular

Gutierrezia. The preferred pollen sources of the female are not known, but probably involve Compositae. Moldenke and Neff (1974) class *S. s. sabinensis* as an "oligolege of sunflowers," but our own observations (LaBerge, 1956a; Cazier and Linsley, 1974) do not bear out this conclusion, although we have taken females gathering pollen from *Helianthus* (Table B and below):

ARIZONA.—COCHISE COUNTY: Cochise, 5 Sep 75, *H. annuus*, 0800-0829, 1♂ (EGL, JML). SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0930-0959, 1♀P (EGL, JML).

58. *Svastra (Epimelissodes) sila* (LaBerge)

Not previously recorded from *Helianthus*, this species is known to occur from Texas to Arizona and southward into Mexico (Baja California and Chihuahua). Although it is an oligolege of Compositae, especially *Baileya pleniradiata* and *Heterotheca psammophila*, we have only found it taking nectar from *Helianthus* (Table B).

59. *Svastra (Epimelissodes) texana* (Cresson)

LaBerge (1956a) recognizes two subspecies, *S. (E.) texana texana* (Cresson), which ranges from eastern Colorado and Kansas south through Oklahoma and Texas, and *S. (E.) texana elula* (LaBerge), which occurs in the desert areas of southern California, Arizona, and northern Mexico (Chihuahua and Coahuila). Females of the former have been taken on *Helianthus* sp. and of the latter on *Helianthus annuus* (see also Tables C and D). The species appears to be an oligolege of Compositae, secondarily associated with *Helianthus*.

Genus *Xenoglossodes* Ashmead

This genus, which occurs only in North America, contains 18 species, of which three have been taken at the flowers of *Helianthus* while seeking nectar. In addition, we have collected a number of specimens, (16♂, 1♀P, 5♀N) representing two or more species at flowers of *Helianthus annuus* in Arizona (Cochise and Santa Cruz Counties) and

New Mexico (Rodeo and Silver City) during September.

60. *Xenoglossodes bishoppi* (Cockerell)

Described originally from a male taken at *Helianthus* in Paris, Texas, this species remains known only from the type specimen.

61. *Xenoglossodes eriocarpi* (Cockerell)

Xenoglossodes eriocarpi is primarily associated with flowers of desert Compositae and ranges from Texas to southern California, but Hurd and Linsley (1975) have recorded a female from *Larrea tridentata*.

We have taken the species in our sunflower surveys as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0859, 4♂ (EGL, JML).

The species evidently visits *Helianthus* for nectar only.

62. *Xenoglossodes helianthorum* Cockerell

Described by Cockerell (1914b) from a male captured on sunflower at Falfurrias, Texas, this species remains known only on the basis of the male.

Genus *Peponapis* Robertson

The bees of this genus occur only in the Western Hemisphere and the females obtain pollen exclusively from squashes, gourds, and pumpkins (*Cucurbita*). While both sexes take nectar chiefly from the flowers of these plants, Hurd and Linsley (1964:380) list a number of other plants that are known to be visited for nectar. Only the following species has been found to visit flowers of *Helianthus*.

63. *Peponapis (Peponapis) pruinosa* (Say)

This species, which ranges from Maine to Georgia, west to Idaho and California, and south into

Mexico (Central Plateau and west coast south to Oaxaca), is an oligolege of uncultivated xerophytic *Cucurbita* including *C. foetidissima* and *C. galleotti* as well as most, if not all domestic *Cucurbita* grown within its range. A nectar-seeking female was taken at the flowers of *Helianthus annuus* (Table M) and two males were collected on the same flower at 7.5 mi N Manteca, San Joaquin County, California, on 21 July 1977, 1100–1129 (EGL, JML, AEM, MMM).

Genus *Melissodes* Latreille

This large genus, although present in both North and South America as well as the West Indies, is especially well represented by numerous species in North America. Of the 99 species known to be present in America north of Mexico, 55 have been taken at the flowers of *Helianthus*. Most of these are oligoleges of the Compositae (38), either primarily (7 species) or secondarily (31 species) associated with *Helianthus*. Of the remaining species (17), 13 are polyleges (six regulars and seven casuals) and four seek only nectar from these flowers.

These bees are among the most important pollinators of sunflower.

64. *Melissodes (Melissodes) bimaculata bimaculata* (Lepeletier)

Recorded by Robertson (1929) from flowers of *Helianthus annuus* (♀N), *H. grosseserratus* (♂, ♀P), and *H. tuberosus* (♀N) in Illinois, LaBerge (1956a) has added *H. divaricatus* to this list. The species ranges from North Dakota to Maine, Florida, Texas, northeastern New Mexico, and eastern Colorado. The other subspecies, *M. b. nulla* LaBerge, occurs in southern Florida and the adjacent Keys, but so far has been found only at flowers of *Lythrum lineare*. The nominate subspecies is apparently a regular polylege of *Helianthus*.

65. *Melissodes (Melissodes) communis communis* Cresson

This subspecies visits a wide range of flowers, including *Helianthus* and other Compositae, along

with members of other plant families. It ranges from Wyoming and North Dakota to the New England States and south to Florida, Chihuahua, and Tamaulipas, Mexico. Recorded specifically from *Helianthus annuus* and *H. lenticularis* (LaBerge, 1958) and *H. debilis* (Graenicher, 1930), this subspecies appears to be a regular polylege of *Helianthus*.

66. *Melissodes (Melissodes) comptoides* Robertson

This species ranges from New Jersey to Florida and west to South Dakota, Colorado, and Arizona (LaBerge, 1956a). It has been recorded from *Helianthus* sp., *H. annuus*, and *H. petiolaris*, but according to LaBerge (1956a) it appears to prefer pollen of *Euphorbia marginata*, *Medicago sativa*, and *Melilotus alba*. *Melissodes comptoides* appears to be possibly a regular polylege of *Helianthus*.

67. *Melissodes (Melissodes) paroselae* Cockerell

This species ranges from southwestern Texas to southeastern California and Mexico (Baja California, Sonora, Chihuahua, and Nayarit). It is polylectic and has been recorded from *Helianthus* sp. and *H. annuus* by LaBerge (1956a). Its relationship with *Helianthus* appears to be that of a casual polylege.

Records for this species at the principal survey sites appear in Tables B-E. Data from additional survey sites are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800–0829, 2♂, 2♀P, 1♀N (EGL, JML). PIMA COUNTY: Marana, 27 Jun 74, *H. annuus*, 1030–1059, 8♂ (AEM, MMM); Rillito, 6 mi W, 27 Jun 74, *H. annuus*, 0830–0929, 10♂, 3♀N (AEM, MMM), 2 Aug 75, *H. annuus*, 0715–0729, 1♂ (AEM, MMM), 12 Aug 75, *H. annuus*, 0930–0959, 1♂ (EGL, JML); Sahuarita, 26 Jun 74, *H. annuus*, 1200–1229, 11♂, 1♀N (AEM, MMM). PINAL COUNTY: Eloy, 30 Jul 75, *H. annuus*, 0915–0929, 1♂ (AEM, MMM). SANTA CRUZ COUNTY: Sonoita, 16 Sep 74, 4♂ (PDH, AEM, MMM).

68. *Melissodes (Melissodes) tepida* Cresson

Of the three subspecies recognized by LaBerge (1956a), two have been reported from *Helianthus*: *M. (M.) tepida tepida* Cresson, ranging from north-

western Oregon and southern Idaho to northern Utah, Nevada, and northern California and *M. (M.) tepida timberlakei* LaBerge, which occurs in southern Oregon and central and southern California. These have been taken on *Helianthus* sp., *H. annuus*, *H. bolanderi*, and *H. petiolaris*. The species is evidently a casual polylege of *Helianthus*.

69. *Melissodes (Melissodes) tessellata* LaBerge

Recorded from *Helianthus* sp. and *H. annuus* in southern California by LaBerge (1956a), this polylectic species ranges from central California to Mexico (Baja California and Jalisco). It appears to be a regular polylege of *Helianthus*.

70. *Melissodes (Melissodes) thelypodii thelypodii* Cockerell

This polylectic subspecies has been collected on *Helianthus annuus* but is more abundant on other plants. It ranges from southern California to southeastern Texas and south to northern Durango (LaBerge, 1956a). Our collection records are recorded in Tables B and C. It appears to be a casual polylege of *Helianthus*.

71. *Melissodes (Apomelissodes) fimbriata* Cresson

This species, which obtains both pollen and most of its nectar supply from flowers of *Oenothera*, ranges from Virginia to Georgia and west to Texas and Kansas. LaBerge (1956b) has recorded the species visiting flowers of *Helianthus petiolaris* for nectar.

72. *Melissodes (Heliomelissodes) desponsa* Smith

The male of this species was recorded from *Helianthus strumosus* in Wisconsin by Graenicher (1909). LaBerge (1956b) adds *H. annuus* and *H. grosseserratus* and Mitchell (1962) includes *Helianthus* among his floral records. It occurs along the Atlantic Coast from Nova Scotia to North Carolina and Alabama and west to North Dakota and Oklahoma. It collects pollen principally from

flowers of *Cirsium* but appears to be a casual polylege of *Helianthus*.

73. *Melissodes (Heliomelissodes) rivalis* Cresson

LaBerge (1956b) reported this species as oligolectic on Compositae, especially *Cirsium*. Among his flower records is *Helianthus annuus*. It ranges from northern California to southern British Columbia, east to southern Manitoba and northwestern Minnesota and south to Texas, New Mexico, and Arizona. It may be secondarily dependent upon *Helianthus*.

74. *Melissodes (Tachymelissodes) opuntiaella* Cockerell

This polylectic species obtains pollen from such flowers as *Cirsium*, *Lindheimera texana*, *Sphaeralcea pedatifolia*, *Verbesina encelioides*, and *Helianthus annuus* according to LaBerge (1956b). It ranges from Texas to California and Utah, south into Mexico (Coahuila, Mexico, and Zacatecas). It is apparently a casual polylege of *Helianthus*.

75. *Melissodes (Tachymelissodes) sonorensis* LaBerge

Melissodes sonorensis was described from specimens taken five and 15 miles south of Navajoa, Mexico, on *Kallstroemia grandiflora* (LaBerge, 1963). We have not found additional published records of collections of this species which is now recorded from the United States (New Mexico). Our data are to be found in Table A and indicate that this species is possibly a regular polylege of *Helianthus*.

76. *Melissodes (Eumelissodes) agilis* Cresson

FIGURE 10; PLATE 4

LaBerge (1961) regards this species as an oligolectic of *Helianthus*. The summary of floral records presented by him clearly indicates a very strong preference for plants of this genus and our field collections clearly support his conclusion. We found it at practically every site sampled. Of

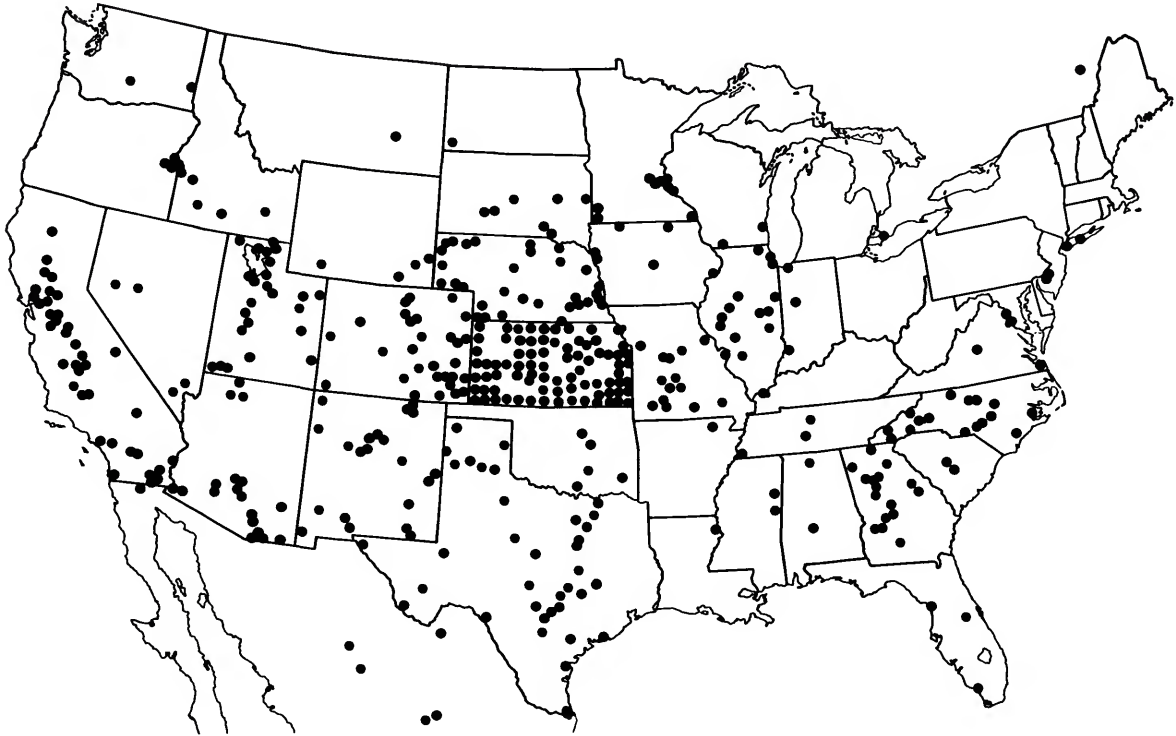


FIGURE 10.—Distribution of *Melissodes (Eumelissodes) agilis* Cresson.

520 females tabulated by LaBerge, 428 were from a species of *Helianthus*, 63 from Compositae other than *Helianthus*, and only 29 from plants other than Compositae. The species ranges throughout the United States (except Florida), southern Canada, and northern Mexico. *Helianthus* species visited include *H. annuus*, *H. atrorubens*, *H. bolanderi*, *H. ciliaris*, *H. coronatus*, *H. divaricatus*, *H. grosseserratus*, *H. laetifloris*, *H. lenticularis*, *H. maximiliani*, *H. mollis*, *H. petiolaris*, *H. pumilus*, *H. radula*, *H. rigidus*, *H. salicifolius*, *H. scaberrimus*, *H. subrhomboides*, and *H. tuberosus*.

Males patrol the flower heads of sunflower throughout the day along with those of *Svastra* spp., *Diadasia enavata*, and other species of *Melissodes*, cruising about the tops of the tallest plants. At night they gather gregariously on flower heads for "sleeping" ranging in numbers from two or three to a very crowded 25 or 30, although some-

times they occur singly. They remain on the flowers until after the sun's rays reach them or until the air temperature is sufficiently high to permit flight. This may be as much as an hour after females have begun collecting pollen.

Graenicher (1909) recorded the species from flowers of *Helianthus strumosus* (♂, ♀P) in Wisconsin and Robertson (1929) found it to visit seven species of *Helianthus* in Carlinville, Illinois, including *H. annuus* (♂, ♀N), *H. divaricatus* (♂, ♀P), *H. grosseserratus* (♂, ♀P, abundant), *H. mollis* (♂, ♀P), *H. rigidus* (♂, ♀P), and *H. tuberosus* (♂, ♀P, frequent). The species is clearly an oligolege of the Compositae, primarily associated with *Helianthus*.

M. agilis was found at all our primary sampling sites (Tables A-M) as well as other collecting areas as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0859, 7♂, 9♀P, 3♀N (EGL, JML). GRAHAM

COUNTY: Franklin, 6 Aug 75, *H. annuus*, 1130–1159, 4♂ (EGL, JML). PIMA COUNTY: San Xavier, 19 Sep 74, on flowers of *H. annuus*, 1200–1259, 1♂, 1♀N (PDH, AEM, MMM). SANTA CRUZ COUNTY: Nogales, 17 Sep 74, *H. annuus*, 1210–1240, 2♂, 4♀P, 4♀N (PDH, AEM, MMM), 15 Sep 77, *H. annuus*, 0700–0759, 13♂, 87♀P, 1600–1629, 1♀P (EGL, JML); Patagonia, 7 Sep 77, *H. annuus*, 0730–0759, 3♂, 16♀P (EGL, JML); Sonoita, 16 Sep 74, *H. annuus*, 3♂ (PDH, AEM, MMM); Sonoita 10 mi E, 7 Sep 77, *H. petiolaris*, 0830–0859, 2♀P (EGL, JML).

CALIFORNIA.—CONTRA COSTA COUNTY: Byron 4 mi E, 21 Jul 77, *H. annuus*, 0800–0829, 12♂, 7♀P (EGL, JML, AEM, MMM). FRESNO COUNTY: Coalinga 10 mi N, 10 Sep 75, *H. annuus*, 1045–1144, 66♂, 2♀P, 1♀N (AEM, MMM); Highway 99, Visalia-Hanford Junction, 22 Aug 76, 0730–0759, 14♀P (AEM, MMM); Parlier, 7 Sep 75, *H. annuus*, 1400–1429, 2♂, 5♀P, 1♀N (EGL, JML, AEM, MMM); Selma, 6 Sep 75, *H. annuus*, 1030, 2♀P, 1♀N (EGL, JML, AEM, MMM). INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0630–0729, 1♂, 36♀P, 0730–0829, 2♂, 14♀P (EGL, JML); Tuttle Creek 4 mi W of Lone Pine, 29 Aug 77, *H. annuus*, 1030–1059, 18♂, 3♀P, 2♀N (EGL, JML). KERN COUNTY: Bakersfield 8 mi S, 22 Aug 76, *H. annuus*, 1030–1059, 2♂, 1♀N (AEM, MMM); Copus Road between Highway 5 and 99, 22 Aug 76, *H. annuus*, 1130–1159, 1230–1259, 4♂ (AEM, MMM); Highway 5 junction with Copus Road, 10 Sep 75, *H. annuus*, 1430–1445, 4♂, 1♀N (AEM, MMM); Highway 5 at Old River Road, 10 Sep 75, *H. annuus*, 1400–1415, 4♂, 1♀N (AEM, MMM). LOS ANGELES COUNTY: Calabasas, 29 Sep 75, *H. annuus*, 0915–0920, 58♂, 3♀N (AEM, MMM); Gorman, 19 Aug 76, *H. annuus*, 0800–0829, 1♂, 4♀P (AEM, MMM). MERCED COUNTY: Atwater, 23 Jul 77, *H. annuus*, 1100–1229, 11♂, 1♀N (EGL, JML, AEM, MMM). ORANGE COUNTY: Newport Beach, 13 Sep 75, *H. annuus*, 1015–1029 (overcast), 14♂, 4♀N, 28♀P (AEM, MMM), 27 Aug 76, *H. annuus*, 1400–1429 (overcast), 23♂, 3♀P, 6♀N (AEM, MMM). RIVERSIDE COUNTY: Blythe, 29 Jun 74, *H. annuus*, 0800–0829, 1♂, 6♀P (AEM, MMM); Coachella, 8 Jun 76, *H. annuus*, 0900–0929, 1♂, 1♀N (EGL, JML); Indio, 8 Jun 76, *H. annuus*, 0700–0829, 6♂, 5♀P, 2♀N (EGL, JML), 1400–1429, 2♂ (EGL, JML). SAN JOAQUIN COUNTY: Manteca 7.5 mi N, 21 Jul 77, *H. annuus*, 1100–1129, 10♂, 7♀N (EGL, JML); Victoria Island, 0.5 E of Old River, 21 Jul 77, *H. annuus* (commercial field), 0930–0959, 16♂, 12♀N, 3♀P (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Ceres, 27 Jul 77, *H. annuus*, 0800–0829, 27♂, 45♀P (EGL, JML, AEM, MMM); Grayson 6.5 mi N, 27 Jul 77, *H. annuus*, 1100–1129, 2♂, 1♀P, 4♀N (EGL, JML, AEM, MMM); Modesto, 3 Sep 75, *H. annuus*, 0745–0815, 21♂, 29♀P, 2♀N (EGL, JML, AEM, MMM); Patterson, 21 Jul 76, *H. annuus*, 1315, 4♂ (AEM, MMM), 27 Jul 77, *H. annuus*, 0930–0959, 2♂, 2♀N, 1♀P (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Sep 75, *H. annuus*, 1200–1230, 6♂, 1♀P, 12♀N (EGL, JML, AEM, MMM); Tulare, 6 Oct 75, *H. annuus*, 1600–1629, 2♂, 1♀N, 5♀P (EGL, JML, AEM, MMM).

77. *Melissodes (Eumelissodes) appressa* LaBerge

This California species is an oligolege of Compositae, especially *Gutierrezia*, *Haplopappus*, and *Heterotheca* (LaBerge, 1961). A nectar-gathering female was taken at flowers of *Helianthus annuus* at Anaheim, California in August by P. H. Timberlake.

78. *Melissodes (Eumelissodes) bidentis* Cockerell

The range of this species extends from North Dakota to New York and south to Texas. Flower records include *Helianthus annuus*, *H. maximiliani*, and *H. tuberosus* and related Compositae (Stevens, 1951b). It is apparently an oligolege of Compositae, secondarily associated with *Helianthus*.

79. *Melissodes (Eumelissodes) bimatrix* LaBerge

LaBerge (1961) reported *M. bimatrix* as an oligolege of Compositae, especially *Chrysothamnus*. His list of flower records includes *Helianthus* sp. The bee is known from British Columbia to southern California and east to Colorado and New Mexico. It appears to be secondarily associated with *Helianthus*.

80. *Melissodes (Eumelissodes) boltoniae* Robertson

Recorded from *Helianthus* sp., *H. annuus*, *H. grosseserratus* and *H. tuberosus* (LaBerge, 1961), the species ranges from Minnesota to North Carolina, Florida, and eastern Texas. It is an oligolege of the Compositae that regularly visits the flowers of *Helianthus*.

81. *Melissodes (Eumelissodes) brevipygga* LaBerge

Recorded from California, Arizona, and Idaho, the flower list provided by LaBerge (1961) suggests that the species may be an oligolege of

Compositae, although it has not previously been reported from *Helianthus*. For our collection data see Table B. It appears to be secondarily associated with *Helianthus*.

82. *Melissodes (Eumelissodes) confusa* Cresson

Melissodes confusa ranges from southern Canada (Alberta, Manitoba, and Saskatchewan) to southern Mexico (Veracruz and Oaxaca). The data of LaBerge (1961) indicate a strong preference for Compositae, but as he emphasized at that time, it had not yet been found on *Helianthus*.

Only males of this species have been taken by us in our surveys shown in Table C and the following:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0829, 1♂ (EGL, JML).

83. *Melissodes (Eumelissodes) coreopsis* Robertson

This species visits plants of a wide variety of genera of Compositae but appears to have a preference for *Helianthus*. Cockerell (1923) recorded the female (as *M. confusiformis*) from *H. annuus lenticularis* at Wray, Colorado. Of 579 floral records for females tabulated by LaBerge (1961), 211 were from *Helianthus*, 54 from *Gaillardia*, 44 from *Rudbeckia*, 36 from *Echinacea*, 22 from *Grindelia*, 15 from *Solidago*, 38 from *Aster*, 25 from *Coreopsis*, 77 females were recorded from other genera of Compositae, and 57 from plants of other families. Species of *Helianthus* visited include *H. annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. salicifolius*, and *H. tuberosus*. The species ranges from Alberta, North Dakota, and Minnesota to Illinois, Texas, and Arizona. It is an oligolege of the Compositae, primarily associated with *Helianthus*.

We have taken both sexes in our surveys; most of the females were collecting pollen. Collection data is recorded in Table C and the following:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800-0829, 2♀P (EGL, JML).

84. *Melissodes (Eumelissodes) denticulata* Smith

This species, which ranges from Quebec west to North Dakota and south to Florida and Texas, is apparently chiefly dependent upon Compositae, especially the genus *Vernonia*, for pollen and nectar. Graenicher (1930:160) has recorded it on *Helianthus debilis* (as *M. perplexa*) and it appears to be a casual polylege of sunflower.

85. *Melissodes (Eumelissodes) dentiventris* Smith

LaBerge (1961) regards this species as primarily associated with Astereae, especially *Aster* and only secondarily with Heliantheae, including *Helianthus annuus*, *H. divaricatus*, *H. grosseserratus*, and *H. radula*. Cockerell (1915c) quoted Rohwer as noting that at Falls Church, Virginia, this species only visits sunflower in the morning, not in the afternoon. Later Cockerell (1917a) recorded both sexes at *Helianthus* in Virginia and a female at the flowers in Connecticut.

Robertson (1929) found the species, which ranges from southeastern Canada to Georgia, the Gulf states, and Texas, visiting three species of *Helianthus* in Carlinville, Illinois, including *H. annuus* (♀N), *H. divaricatus* (♂, ♀P), *H. grosseserratus* (♂, ♀P, frequent).

86. *Melissodes (Eumelissodes) gelida* LaBerge

LaBerge (1961) regarded *M. gelida* as an oligolege of Compositae with some preference for *Helianthus*, as indicated by 7 of 20 females and 14 of 55 males bearing flower data in material studied by him. The species ranges from Montana and North Dakota to New Mexico and Texas. *Helianthus* species visited include *H. annuus* and *H. petiolaris*. Possibly *M. gelida* is primarily associated with *Helianthus*.

87. *Melissodes (Eumelissodes) grindeliae* Cockerell

This species, an oligolege of Compositae, secondarily associated with *Helianthus*, ranges from

Minnesota and North Dakota west through Wyoming, Colorado, and New Mexico to California and Washington (LaBerge, 1961).

**88. *Melissodes (Eumelissodes) humilior*
Cockerell**

This species, although known to visit various Compositae (LaBerge, 1961), has not been recorded from sunflower previously (Table B). It is apparently an oligolege of Compositae, secondarily associated with *Helianthus* and ranges from western Texas to Arizona and south into Mexico (Chihuahua).

**89. *Melissodes (Eumelissodes) illata* Lovell and
Cockerell**

An oligolege of Compositae, secondarily associated with *Helianthus*, it seems to prefer especially species of *Solidago* and *Aster*. It has been recorded as a visitor to *Helianthus strumosus* (LaBerge, 1961), and ranges from Prince Edward Island to Alberta and south to North Carolina (in the mountains) and Illinois.

90. *Melissodes (Eumelissodes) limbus* LaBerge

Although this species is an oligolege of Compositae, especially *Verbesina*, *Haplopappus*, and *Baileya*, LaBerge (1961) remarked that it had not yet been collected on *Helianthus*, a genus frequented by most species of the subgenus *Eumelissodes*. Although we have now taken it on *H. annuus*, the specimens involved were all males (Table B) and further investigation may establish more precisely its relationship with sunflowers.

**91. *Melissodes (Eumelissodes) lutulenta*
LaBerge**

According to LaBerge (1961), this species is an oligolege of the Compositae and seems to prefer *Chrysothamnus*, *Grindelia*, and *Solidago*. Included among his flower records are *Helianthus* sp.; Moldenke and Neff (1974) record it from *Helianthus* in Contra Costa County, California. The species

is primarily an inhabitant of western North America, ranging from British Columbia to Saskatchewan and south to California, Arizona, and Mexico (Guanajuato). It seems to be secondarily associated with *Helianthus*.

**92. *Melissodes (Eumelissodes) menuachus*
Cresson**

Recorded from *Helianthus* sp. (Cockerell, 1906a), *H. grosseserratus* (♀N) (Robertson, 1929), and *H. annuus*, *H. petiolaris*, and *H. grosseserratus* (LaBerge, 1961), the species ranges from British Columbia, Alberta, and North Dakota south to Illinois, Texas, California, and into north-central Mexico (Chihuahua and Zacatecas).

We have taken it in a number of principal sample sites (Tables A-E), as well as:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, 0830-0859, 1♂ (EGL, JML).

The species is an oligolege of the Compositae, secondarily associated with *Helianthus*.

**93. *Melissodes (Eumelissodes) microsticta*
Cockerell**

This is an oligolege of Compositae that visits *Helianthus* especially in the Utah-Wyoming areas of its range, which includes British Columbia to Saskatchewan and south to California, Nevada, Utah, and Texas (LaBerge, 1961). It is apparently secondarily associated with *Helianthus*.

**94. *Melissodes (Eumelissodes) montana*
Cresson**

This species is an oligolege of Compositae secondarily associated with *Helianthus*. It has been collected from flowers of *Helianthus* sp. and *H. annuus* (LaBerge, 1961). The species ranges from Colorado and Utah south to Mexico (Oaxaca and Baja California).

Both sexes, including pollen-collecting females, have been taken by us in primary sampling sites in New Mexico and Arizona (Tables A-E) as well as additional sites as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830–0859, 2♀P (EGL, JML). SANTA CRUZ COUNTY: Nogales, 17 Sep 74, *H. annuus*, 1210–1240, 1♀P (PDH, AEM, MMM), 15 Sep 77, *H. annuus*, 0930–0959, 1♀P (EGL, JML); Sonoita, 16 Sep 74, *H. annuus*, 8♂, 1♀ (PDH, AEM, MMM); Sonoita 10 mi E, 7 Sep 77, *H. petiolaris*, 0830–0859, 1♀N (EGL, JML).

95. *Melissodes (Eumelissodes) nivea* Robertson

Regarded by LaBerge (1961) as an oligolege of Compositae, it has been captured at flowers of *Helianthus* sp., *H. annuus*, and *H. atrorubens* and appears to be secondarily associated with sunflowers. The species ranges from New York to North Carolina and west to Mississippi, Kansas, and Minnesota. Robertson (1929) found the species visiting two species of *Helianthus* in Carlinville, Illinois, including *H. divaricatus* (♂) and *H. grosseserratus* (♂, ♀N).

96. *Melissodes (Eumelissodes) pallidesignata* Cockerell

LaBerge (1961) reported this species as an oligolege of Compositae depending primarily on the flowers of *Chrysothamnus*, *Grindelia*, and *Haplopappus*. *Helianthus* is included among his flower records. Thorp and Chemsak (1964) have described the nesting habits and adult behavior in coastal California, where females were gathering pollen from *Grindelia stricta* and *Erigeron glaucus*. It appears to be secondarily associated with *Helianthus*.

97. *Melissodes (Eumelissodes) paulula* LaBerge

Melissodes paulula is regarded by LaBerge (1961) as an oligolege of Compositae that appears to prefer *Gutierrezia*, *Haplopappus*, and *Solidago*, as borne out by his tabular summary of floral data. Included among his lesser flower records is *Helianthus annuus*, and Moldenke and Neff (1974) cite a male from this sunflower from Riverside County, California. The species occurs from Washington to southern California but is primarily confined to California. It is evidently secondarily associated with *Helianthus*.

98. *Melissodes (Eumelissodes) perlusa* Cockerell

LaBerge (1961) suggests that *M. perlusa* is probably an oligolege of Compositae. He recorded the species from *Helianthus* sp., *H. annuus*, and *H. petiolaris*. Of 38 collections (58 bees) with flower data examined by him, 23 collections (12 females and 28 males) were made on *Helianthus*, mostly *H. petiolaris*. The species ranges from Alberta and Manitoba south to Iowa and Arizona. It appears to be an oligolege of the Compositae possibly associated primarily with *Helianthus*.

99. *Melissodes (Eumelissodes) robustior* Cockerell

This is a species of western North America, ranging from Washington and Idaho to southern California and northern Nevada. It is an oligolege of Compositae, primarily associated with *Helianthus*. Of 148 females included by LaBerge (1961) in his tabulation of flower records, 60 were from *Helianthus*. Species included were *Helianthus annuus*, *H. bolanderi*, *H. gracilentus*, *H. lenticularis*, and *H. petiolaris*. Chemsak and Thorp (1962) have described the sleeping habits of males on fresh flowers of *Scabiosa atropurpurea* and *Cosmos bipinnatus* in August and September at Berkeley, California. Females were taking pollen from *Cosmos*.

This species was collected at *H. annuus* at one primary sampling site in California (Table K) as well as additional localities as follows:

CALIFORNIA.—FRESNO COUNTY: Parlier, 7 Oct 75, *H. annuus*, 1400–1429, 2♂ (EGL, JML, AEM, MMM). IMPERIAL COUNTY: El Centro, 29 Jul 75, *H. annuus*, 1000–1029, 5♂ (AEM, MMM); Holtville 3 mi W, 29 Jul 75, *H. annuus*, 1100–1114, 1♂ (AEM, MMM). KERN COUNTY: Highway 5 at Old River Road, 10 Sep 75, *H. annuus*, 1400–1415, 2♂ (AEM, MMM); Highway 5 and Junction of Copus Road, 10 Sep 75, *H. annuus*, 3♂ (AEM, MMM). STANISLAUS COUNTY: Patterson, 27 Jul 77, *H. annuus*, 0930–0959, 3♂, 3♀P (EGL, JML, AEM, MMM).

100. *Melissodes (Eumelissodes) rustica* (Say)

This species is primarily associated with *Solidago*, *Aster*, and *Grindelia*, but has been reported

from *Helianthus* sp., *H. atrorubens*, *H. divaricatus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, *H. radula*, and *H. tuberosus* (LaBerge, 1961). The species ranges from Nova Scotia south to Louisiana, west to Idaho and New Mexico, and south into Mexico. It is an oligolege of the Compositae, secondarily associated with *Helianthus*.

In Wisconsin, Graenicher (1909) found males visiting flowers of *Helianthus strumosus* and in Illinois Robertson (1929) found males visiting *H. divaricatus*, *H. grosseserratus*, and *H. tuberosus*. Clement (1973) has described the nesting habits and larva of this species.

101. *Melissodes (Eumelissodes) snowii* Cresson

LaBerge (1961) regards this species as probably an oligolege of Compositae. Females have been taken most often on *Helianthus*, including *Helianthus* sp., *H. petiolaris*, and *H. subrhomboides*. The species ranges over the western part of the Great Plains including Alberta, Manitoba, Colorado, New Mexico, Nebraska, and North Dakota. It seems to be secondarily associated with *Helianthus*.

102. *Melissodes (Eumelissodes) subagilis* Cockerell

Melissodes subagilis is mainly found at Compositae, although LaBerge (1961) does include other families among his flower records. For *Helianthus*, he lists *H. sp.*, *H. annuus*, *H. maximiliani*, and *H. petiolaris*. It appears to be an oligolege of Compositae, secondarily associated with *Helianthus*. For records of our collections see Tables B and D.

103. *Melissodes (Eumelissodes) subillata* LaBerge

This species is an oligolege of Compositae and has been recorded from flowers of *Helianthus maximiliani* and *H. petiolaris* (LaBerge, 1961). It ranges from Quebec to Saskatchewan and south to Illinois and North Carolina. It appears to be secondarily associated with *Helianthus*.

104. *Melissodes (Eumelissodes) submenuacha* Cockerell

LaBerge (1961) regarded this species as probably an oligolege of Compositae. Cockerell (1906b) reported it from *Helianthus* at Albuquerque, New Mexico, and LaBerge's flower records include a female and male at *Helianthus annuus* at Las Cruces and Mesilla Park, New Mexico, respectively, and both sexes at *H. petiolaris* at Carrizozo, New Mexico. The range includes Colorado and southeastern Arizona, New Mexico and western Texas. It appears to be an oligolege of Compositae, secondarily associated with *Helianthus*.

For data from principal sampling sites, see Tables B, C, and E. Additional records are as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus* (♂ flowers), 0800–0829, 4♀P (EGL, JML). SANTA CRUZ COUNTY: Sonoita, 16 Sept 74, *H. annuus*, 3♂ (PDH, AEM, MMM).

NEW MEXICO.—DONA ANA COUNTY: Mesilla Park, 5 Sep 61, *H. annuus*, ♂ (PDH). LINCOLN COUNTY: Carrizozo, 10 Sep 61, *H. petiolaris*, 2♀N (PDH).

105. *Melissodes (Eumelissodes) tincta* LaBerge

An oligolege of Compositae, especially *Chrysoopsis* and *Aster*, this species has also been taken at flowers of *Helianthus maximiliani* (LaBerge, 1961). It ranges from Minnesota and Michigan south to Florida and Texas. It appears to be secondarily associated with *Helianthus*.

106. *Melissodes (Eumelissodes) trinodis* Robertson

FIGURE 11

LaBerge (1961) regards this species as an oligolege of Compositae primarily associated with *Helianthus*. His table of floral records supports this conclusion, although he had flower data for only 47 females. Of these, 30 were from species of *Helianthus*, 13 from Compositae other than *Helianthus*, and 4 from plants other than Compositae. The species ranges from southeastern Canada and Maine south to Georgia and west to North

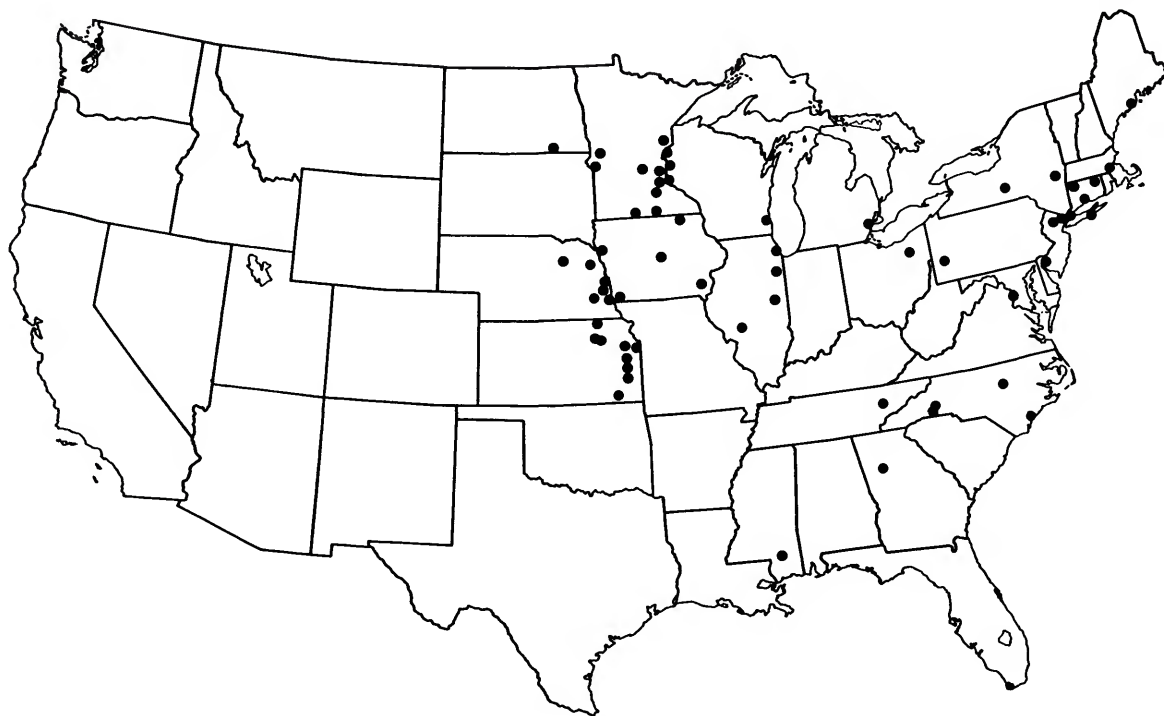


FIGURE 11.—Distribution of *Melissodes (Eumelissodes) trinodis* Robertson.

Dakota and Kansas. *Helianthus* records include *H. annuus*, *H. atrorubens*, *H. divaricatus*, *H. grosseserratus*, *H. maximiliani*, *H. mollis*, *H. salicifolius*, and *H. tuberosus*. Graenicher (1909) recorded the species in Wisconsin from *Helianthus giganteus* (♂, ♀P) and *H. strumosus* (♂, ♀P) and Robertson (1929) found it visiting five species in Carlinville, Illinois, including *H. annuus* (♂, ♀P), *H. divaricatus* (♂, ♀P), *H. grosseserratus* (♂, ♀P, frequent), *H. mollis* (♀P), and *H. tuberosus* (♂, ♀N, frequent). The species is parasitized by *Triepeolus helianthi* (Graenicher, 1905), which is also a frequent visitor to sunflowers.

**107. *Melissodes (Eumelissodes) tristis*
Cockerell**

This is the most polylectic species of the subgenus *Eumelissodes*, visiting plants of a wide range of families and seeming to prefer flowers of the Leguminosae, Compositae, and Malvaceae. It has been recorded from *Helianthus* sp., *H. annuus*, *H. ciliaris*, and *H. petiolaris*. The range includes

Nebraska to California and south through Texas, New Mexico, and Arizona to southern Mexico (Oaxaca).

Our numerous sunflower records are all based upon nectar seeking individuals of both sexes. It appears to be a casual polylege of *Helianthus*.

For data from primary survey sites see Tables A–E; additional samples are as follows:

ARIZONA.—GRAHAM COUNTY: Franklin, 6 Aug 75, *H. annuus*, 1130–1159, 1♂ (EGL, JML). PIMA COUNTY: Rillito, 6 mi W, 27 Jun 74, *H. annuus*, 0900–0929, 1♂, 1♀N (AEM, MMM), 30 Jul 75, *H. annuus*, 1330–1529, 10♂ (EGL, JML, AEM, MMM), 2 Aug 75, *H. annuus*, 0715–0729, 1♂ (AEM, MMM); Sahuarita, 26 Jun 74, *H. annuus*, 1200–1229, 22♂ (AEM, MMM). PINAL COUNTY: Eloy, 30 Jul 75, *H. annuus*, 1♂ (AEM, MMM). SANTA CRUZ COUNTY: Sonoita, 16 Aug 74, 3♂ (PDH, AEM, MMM).

**108. *Melissodes (Eumelissodes) velutina*
Cockerell**

Melissodes velutina females appear to prefer species of Polemoniaceae (LaBerge, 1961) although

Compositae are visited by the species including *Helianthus gracilentus* (by males). The species is limited to central and southern California (LaBerge, 1961), and is considered as a nectar visitor to *Helianthus*.

**109. *Melissodes (Eumelissodes) verbesinarum*
Cockerell**

LaBerge (1961) records the known range of *M. verbesinarum* as from Washington to southern California, east to Nevada and Texas, and south to Jalisco, Mexico. He regards it as an oligolege of Compositae, but *Helianthus* is not included in his records. Our *Helianthus* records involve only males (Table B).

**110. *Melissodes (Eumelissodes) vernoniae*
Robertson**

Although primarily an oligolege of *Vernonia* (345 of 380 females tabulated by LaBerge (1961) were from plants of this genus), it has been recorded from *Helianthus* sp. and *H. tuberosus*. The species ranges from Indiana and North Dakota west to Idaho and south to New Mexico and Texas. It appears to be secondarily associated with *Helianthus*.

**111. *Melissodes (Eumelissodes) wheeleri*
Cockerell**

An oligolege of Compositae, especially *Gaillardia*, *Helianthus*, and *Rudbeckia* in that order (LaBerge, 1961), it has been recorded from *H. annuus*, *H. debilis*, and *H. petiolaris*. The range includes Michigan and North Dakota south to Louisiana, Texas, and Arizona. It evidently is secondarily associated with *Helianthus*.

**112. *Melissodes (Callimelissodes) coloradensis*
Cresson**

Recorded from *Helianthus* sp., *H. annuus*, *H. atrorubens*, *H. divaricatus*, *H. grosseserratus*, *H. mollis*, *H. petiolaris*, *H. scaberrimus*, and *H. tuberosus* (LaBerge, 1961), this species ranges from Wisconsin to North Carolina and west to Arizona, Utah,

and Wyoming. Robertson (1929) found *M. coloradensis* visiting six species of *Helianthus* in Carlinville, Illinois, including *H. annuus* (♂, ♀P), *H. divaricatus* (♂, ♀P, frequent), *H. grosseserratus* (♀P), *H. rigidus* (♀P), and *H. tuberosus* (♂, ♀P, frequent). LaBerge (1961) reports *Helianthus* serves as the primary source of pollen.

**113. *Melissodes (Callimelissodes) composita*
Tucker**

This species ranges from Montana south to New Mexico and Arizona. LaBerge (1961) noted a preference for Compositae but his list of flower records did not include *Helianthus*. Our data indicate this species to be an oligolege of Compositae secondarily associated with *Helianthus*.

In addition to sunflower pollen collecting data in Tables B and D, we have one record as follows:

ARIZONA.—SANTA CRUZ COUNTY: Sonoita, 16 Aug 74, *H. annuus*, 1♀N (PDH, AEM, MMM).

Hurd and Linsley (1959) report the species using a common entrance to reach their nests which are made individually from subsoil cracks. They also report that *Triepeolus helianthi* Robertson may be a parasite of this species as many were found about the nesting site as well as at the same flowers being visited by *M. composita*.

**114. *Melissodes (Callimelissodes)*
glenwoodensis Cockerell**

This species ranges from North Dakota to New Mexico and west to Washington and southern California. It has been recorded from *Helianthus* sp. and *H. petiolaris* as well as other Compositae (LaBerge, 1961) and appears to be secondarily associated with *Helianthus*.

**115. *Melissodes (Callimelissodes) lupina*
Cresson**

Melissodes lupina is a western species ranging from Montana to Washington and south through Colorado, Utah, Nevada, and California to Baja California. LaBerge (1961) regards the species as oligolectic on Compositae and in his summary of

flower records Compositae were involved in 225 of 290 collections, including 436 of 499 females and 223 of 288 males. Included in his flower list are *Helianthus* sp., *H. annuus*, and *H. gracilentus*. In California, Moldenke and Neff (1974) have recorded both sexes from *H. nuttallii* and *H. gracilentus*. The species is an oligolege of Compositae, secondarily associated with *Helianthus*.

In addition to the data in principal sampling sites (Tables H, J–M), we have taken this species at sunflowers as follows:

CALIFORNIA.—FRESNO COUNTY: Parlier, 7 Sep 75, *H. annuus*, 1400–1429, 1♂, 2♀N (EGL, JML, AEM, MMM). KERN COUNTY: Highway 5 at Copus Road, 10 Aug 75, *H. annuus*, 1430–1445, 6♂ (AEM, MMM); Highway 5 and Old River Road, *H. annuus*, 1400–1415, 5♂ (AEM, MMM). STANISLAUS COUNTY: Patterson, 27 Jul 77, *H. annuus*, 0930–0959, 1♀P (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Sep 75, *H. annuus*, 1200–1230, 3♂ (EGL, JML, AEM, MMM).

**116. *Melissodes (Callimelissodes) lustra*
LaBerge**

Recorded by LaBerge (1961) from *Helianthus* sp. but preferring *Gutierrezia*, *Chrysothamnus*, and *Haplopappus (Isocoma)*, in that order, this species occurs in Idaho, Oregon, Nevada, California, and Mexico (Baja California). It appears to be secondarily associated with *Helianthus*.

**117. *Melissodes (Callimelissodes) plumosa*
LaBerge**

A male doubtfully referred to this species by LaBerge (1961) was taken on *Helianthus petiolaris* at Marmarth, North Dakota. It is otherwise known from California, Oregon, and Washington.

**118. *Melissodes (Callimelissodes) stearnsi*
Cockerell**

This is a Pacific Coast species ranging from Washington to California. Among the flower records provided by LaBerge (1961) are a number of Compositae, including *Helianthus* sp. and *H. annuus*. The female has been collected taking pol-

len from *Helianthus annuus* in Riverside, California, by P. H. Timberlake in August. It is possibly an oligolege of Compositae, secondarily associated with *Helianthus*.

Genus *Martinapis* Cockerell

This genus contains three species, two in North America and one in South America. Both of the North American species are polyleges and only the species treated below has been taken at sunflower.

**119. *Martinapis (Martinapis) occidentalis*
Zavortink and LaBerge**

According to Zavortink and LaBerge (1976), the females of this species are polylectic and are known to collect pollen from plants in the Compositae, Leguminosae, Solanaceae, and Zygophyllaceae. Among the flower records listed by them is one male from *Helianthus niveus*.

Genus *Anthophora* Latreille

Species of this genus are well represented in the Holarctic, Ethiopian, Oriental, and Neotropical Regions. Three subgenera are found in America north of Mexico, of which only *Anthophora* proper and *Micranthophora* contain species that visit sunflowers. Although 63 species of the genus *Anthophora* are present in America north of Mexico, only seven species are known to visit the flowers of *Helianthus*. Most of these are casual polyleges and the others apparently seek nectar only from these flowers.

**120. *Anthophora (Anthophora) montana*
Cresson**

Anthophora montana is a southwestern species ranging from Texas to Colorado, New Mexico, and Arizona. The floral relationships of the females are not well known. Linsley and Hurd (1959) observed them taking pollen from *Mentzelia pumila* in southeastern Arizona as the flowers began to open at about 1540 hrs and continuing

until 1912 hrs when a storm caused cessation of all bee activity. At other times of day they were seen taking nectar from *Asclepias*, *Monarda*, *Helianthus*, and other flowers in the vicinity. For our collection records on *Helianthus annuus*, see Tables B and C. The species appears to be a casual polylege of *Helianthus*.

**121. *Anthophora (Anthophora) smithii*
Cresson**

This is a species ranging from South Dakota and Kansas to Texas, New Mexico, and Arizona. We have taken a single male on sunflower (Table B) and this species is considered to be a nectar visitor to *Helianthus*.

**122. *Anthophora (Anthophora) urbana urbana*
Cresson**

A female of this highly polylectic species has been recorded from *Helianthus annuus* in Stanislaus County and males from *H. gracilentus* in San Bernardino, Riverside, and San Diego counties, California, by Moldenke and Neff (1974). It ranges from Washington and Idaho to New Mexico, Arizona, California, and northwestern Mexico; Mayer and Johansen (1976) have given an account of its habits. Other subspecies have been named from the coastal southern California islands.

Data from our primary sunflower surveys (Tables C and H-M) as well as the following sampling data indicate that this species, although a frequent visitor, does not take pollen from sunflowers.

CALIFORNIA.—CONTRA COSTA COUNTY: Byron, 21 Jul 77, *H. annuus*, 1100-1129, 2♀N (EGL, JML, AEM, MMM). INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0700-0729, 1♀N (EGL, JML). KERN COUNTY: Highway 5 at Copus Road, 10 Aug 75, *H. annuus*, 1430-1445, 1♂ (AEM, MMM); Wheeler Ridge, 23 Sep 76, *H. annuus*, 1245, 10♂ (AEM, MMM). SAN JOAQUIN COUNTY: Manteca 7.5 mi N, 21 Jul 77, *H. annuus*, 1100-1129, 1♀N (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Grayson 6.5 mi N, 21 Jul 77, *H. annuus*, 1130-1159, 1♀N (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Sep 75, *H. annuus*, 1200-1229,

4♂ (EGL, JML, AEM, MMM); Tulare, 6 Sep 75, *H. annuus*, 1600-1629, 2♂ (EGL, JML, AEM, MMM).

Thus this subspecies visits the flowers of *Helianthus* for nectar only.

**123. *Anthophora (Anthophora) walshii*
Cresson**

This species, usually associated with *Cassia*, has been recorded taking nectar from *Helianthus groseserratus* in Illinois by Robertson (1929) and at flowers of *H. petiolaris* in North Dakota by Stevens (1951b). The species has been recorded from Massachusetts, Wisconsin, Illinois, Iowa, Nebraska, Kansas, Colorado, Texas, and doubtfully from Arizona.

**124. *Anthophora (Micranthophora) curta*
Provancher**

This species ranges from Colorado and Texas to California and Baja California, Mexico. Moldenke and Neff (1974) regard the females as pollen specific to Compositae. They record one female and 9 males from *Helianthus gracilentus* in San Diego County, California, males from *H. annuus* and *H. sp.* in Riverside County. Two subspecies have been recognized, *A. c. curta* and *A. c. melanops* Cockerell, but the character given for the latter by Cockerell does not hold up in our material.

Records from major survey sites are presented in Tables A, B, H, and K. In addition it was taken at sunflower as follows:

CALIFORNIA.—SAN DIEGO COUNTY: Highway 8 at Laguna Junction, 13 Jun 74, *H. annuus*, 1300-1415, 2♂, 3♀N, 1♀P (AEM, MMM).

It appears to be a casual polylege of *Helianthus*.

**125. *Anthophora (Micranthophora)*
maculifrons Cresson**

Cockerell (1898a) recorded this species from *Helianthus annuus* in New Mexico. The range extends westward to Nevada and Baja California. Moldenke and Neff (1974) record pollen-bearing

females from *Chrysothamnus* and regard it as an oligolege of this genus of plants. More likely it is an oligolege of Compositae but too few records are available to judge. It appears to be a casual polylege of *Helianthus*.

**126. *Anthophora (Micranthophora) peritomae*
Cockerell**

Cockerell (1907b) has recorded the female of this species from *Helianthus annuus* at Las Cruces, New Mexico. The known occurrence also includes Wyoming, Colorado, and Utah. In this last state, Torchio (1971) has reported females storing pollen from *Grindelia squarrosa*. It appears to be a casual polylege of *Helianthus*.

Genus *Xeromelecta* Linsley

Two species of this American genus of cleptoparasitic bees have been taken at sunflowers as detailed below.

**127. *Xeromelecta (Melectomorpha) californica*
(Cresson)**

This cleptoparasite was recorded from *Helianthus lenticularis* at Orange, California, by Cockerell (1916a) and from *H. sp.* in Nebraska by Swenk (1907). Timberlake made the following collections:

CALIFORNIA.—ORANGE COUNTY: Anaheim, 14 Aug 25, *H. annuus*, 1♂ (P. H. Timberlake). RIVERSIDE COUNTY: Idyllwild 13 mi N, San Jacinto Mountains, 23 Jul 63, *H. petiolaris*, 3♂, 2♀ (P. H. Timberlake); The Gavilan, 4 Jun 50, *H. gracilentus*, 1♂ (P. H. Timberlake).

The species ranges widely through central and western North America where it has been associated with the nests of many species of *Anthophora* and has a wide variety of floral hosts. In our surveys it was frequently found at sunflowers along with one of its hosts, *Anthophora urbana*. For collection data at major sites see Tables I and J. It was collected as follows:

CALIFORNIA.—KERN COUNTY: Wheeler Ridge, 23 Sep 76, *H. annuus*, 1245, 1♂ (AEM, MMM). SAN DIEGO COUNTY:

Highway 8 at Laguna Junction, 13 Jun 74, *H. gracilentus*, 1300–1415, 3♀ (AEM, MMM).

**128. *Xeromelecta (Melectomorpha) interrupta*
(Cresson)**

A cleptoparasitic bee ranging from the Central and Rocky Mountain states to Arizona, New Mexico, and Texas and south into north central Mexico (Hurd, 1953). Hurd and Linsley (1975) have recorded it from flowers of *Larrea tridentata*. Our sunflower collections appear in Tables B and C.

Genus *Centris* Fabricius

Most of the species included in this genus occur in the Neotropical Region, but a number of these (22) either occur in America north of Mexico or extend into the United States from Mexico or Central America. Only two of these have been taken at sunflowers, which they visit only for nectar.

129. *Centris (Paracentris) atripes* Mocsary

A polylectic species ranging widely from the southwestern United States (Texas to southern California) to Central America (Costa Rica). It has not been previously recorded from *Helianthus*. In addition to collections at a principal sampling site (Table C), we have taken it as follows:

ARIZONA.—SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0900–0929, 1♂ (EGL, JML).

**130. *Centris (Paracentris) caesalpiniae*
Cockerell**

Centris caesalpiniae is a desert species that occurs in Texas, New Mexico, Arizona, and northern Mexico (Chihuahua). It has not been recorded previously from *Helianthus*, but a single male is listed from *H. annuus* in Table C.

Genus *Ceratina* Latreille

These bees are found on all continents and many of the islands. Thirteen of the 21 species

known from America north of Mexico have been taken at flowers of *Helianthus* including the successfully adventive *C. dallatorreana* from the western Palaearctic, which visits these flowers for nectar only. Otherwise all of our native species are casual polyleges of this plant, except *C. tejonensis*, which appears to seek nectar only.

**131. *Ceratina (Zadontomerus) acantha*
Provancher**

Ceratina acantha is a highly polylectic species ranging from British Columbia and Idaho to Utah, Nevada, California, and Baja California Norte, Mexico. Daly (1973) lists the species from *Helianthus* sp. and Moldenke and Neff (1974) record it from *H. gracilentus*. It appears to be a casual polylege of *Helianthus*.

**132. *Ceratina (Zadontomerus) apacheorum*
Daly**

This is a southwestern species ranging from New Mexico to Nevada and southern California. Daly (1973) provides numerous flower records, including many from Compositae, but it has apparently not been recorded previously from *Helianthus*. The single collection in our sunflower survey was as follows:

CALIFORNIA.—SAN DIEGO COUNTY: Highway 8 at Laguna Junction, 13 Jun 74, *H. annuus*, 1300–1415, 2♂ (AEM, MMM).

It is apparently a casual polylege of *Helianthus*.

**133. *Ceratina (Zadontomerus) calcarata*
Robertson**

Among the flowers in the long list of hosts for males of this bee provided by Daly (1973) is *Helianthus* sp. It ranges throughout most of the eastern United States east of the Rocky Mountains. It may be a casual polylege of *Helianthus*.

134. *Ceratina (Zadontomerus) dupla* Say

Ceratina dupla is a highly polylectic species ranging from Quebec to Florida, west to Manitoba,

and south to Texas, Louisiana, and Mississippi. Among the many floral records provided by Robertson (1929) is *Helianthus annuus* (♀P), *H. divaricatus* (♂, ♀P), and *H. strumosus* (♀N). Graenicher (1909) lists it from *H. strumosus* (♀P). Daly (1973) also records a male from *Helianthus*. It appears to be a casual polylege of *Helianthus*.

135. *Ceratina (Zadontomerus) micheneri* Daly

Ceratina micheneri is presently known from California and Oregon. Among the flower visits recorded by Daly (1973) are a male and two females at *Helianthus* from Westwood Hills, Los Angeles County, California, in February. It may be a casual polylege of *Helianthus*.

**136. *Ceratina (Zadontomerus) nanula*
Cockerell**

This is a western species ranging from British Columbia to Montana and southward to California, Arizona, New Mexico, and northern Mexico. Among the flower records listed by Daly (1973) for females is *Helianthus petiolaris*; for males, *Helianthus* sp. It appears to be a casual polylege of *Helianthus*.

**137. *Ceratina (Zadontomerus) neomexicana*
Cockerell**

A western species occurring from Texas to California, Colorado, and Idaho, *C. neomexicana* is apparently polylectic. Daly (1973) lists a female from flowers of *Helianthus petiolaris* at Artesia, Moffat County, Colorado, in July. It appears to be a casual polylege of *Helianthus*.

138. *Ceratina (Zadontomerus) pacifica* Smith

Daly (1973) records a series of four females and one male captured on *Helianthus petiolaris* in Colorado by C. D. Michener and a female taken on *H. sp.* in Utah by G. E. Bohart. The species is polylectic and widespread in Western North America (British Columbia to California, east to Idaho and Wyoming south to Arizona). It has

been taken once on *H. annuus*. It evidently is a casual polylege of *Helianthus*.

**139. *Ceratina (Zadontomerus) punctigena*
Cockerell**

A California species for which Daly (1973) lists many flower records including *Helianthus occidentalis* and *H. gracilentus*. It appears to be a casual polylege of *Helianthus*.

140. *Ceratina (Zadontomerus) shinersi* Daly

Thus far this species is known only from Texas. Daly (1973) lists a female from *Helianthus annuus* 6 miles north of Raymondville, Willacy County, in April and a male from *H. annuus* 25 mi E. of McKinney, Collin County, in August. It evidently is a casual polylege of *Helianthus*.

141. *Ceratina (Zadontomerus) strenua* Smith

Females of this widespread species of Eastern North America (New York to Georgia and west to Wisconsin, Missouri, Kansas, Oklahoma, and Texas) visit a large range of flowers, including *Helianthus* (Daly, 1973). It appears to be a casual polylege of *Helianthus*.

**142. *Ceratina (Zadontomerus) tejonensis*
Cresson**

This is a Pacific Coastal species occurring in California and Oregon. The females are apparently polylectic. Daly (1973) has listed a male at flowers of *Helianthus gracilentus* at Mt. Santiago, Orange County, California, in September.

**143. *Ceratina (Euceratina) dallatorreana*
Friese**

This species is a native of the Mediterranean Region and is adventive in California, where it reproduces by thelytokous parthenogenesis (Daly, 1966, 1973). Our single capture of a nectar gathering female is reported in Table M.

Genus *Xylocopa* Latreille

This is a very large genus of carpenter bees that is especially well represented in the tropical and subtropical regions of both the Old and New Worlds. A few species occur or extend into the warm temperate regions of both the northern and southern hemispheres and, insofar as is known, all the species are polyleges, many visiting the flowers of both native and introduced plants. There are about 100 species in the Western Hemisphere and prior to this study only a single species, *X. mordax* Smith of the West Indies, had been taken at the flowers of *Helianthus*, apparently seeking nectar (Hurd, 1978). Even though there are nine species of *Xylocopa* present in America north of Mexico and some of them very abundant in areas where sunflowers grow, only the two subspecies of *X. californica* listed below have been found at these flowers, each on a single occasion questing for nectar.

Since this study was completed, one of us (PDH) had an opportunity to observe the Old World *X. (Koptortosoma) pubescens* Spinola visiting flowers of an ornamental sunflower (*Helianthus annuus*) growing under introduced conditions in the home garden of Dr. Dan Gerling in Tel-Aviv, Israel. Although during the period of these observations (20 July–7 August 1978) there were a number of competing sources of pollen and nectar (e.g., *Carica*, *Cleome*, and *Luffa*) in that garden, not to mention other nearby sources, both sexes of this carpenter bee were commonly observed sipping nectar from these sunflowers and occasionally the females collected pollen, especially in the morning before 0900 hrs.

On 16 September 1978 and again two days later, males of *X. virginica texana* Cresson (one in each instance) were observed (Hurd) taking nectar from flowers of *H. annuus* in Austin, Texas. No females were seen at these flowers during the month and, although females of two other carpenter bees (*X. micans* Lepeletier and *X. tabaniformis parkinsoniae* Cockerell) collected pollen from flowers of *Solanum elaeagnifolium* and *S. rostratum* growing among and adjacent to *H. annuus*, they did not visit the sunflowers.

**144. *Xylocopa (Xylocopoides) californica*
Cresson**

Three subspecies of *X. californica* occur within the range of *Helianthus*, but only two of these have been taken at these flowers. For *X. c. arizonensis* Cresson, which ranges across the deserts of southwestern United States (western Texas to Utah, Nevada, and southern California) south into Mexico (Hurd, 1955, 1961), we record:

NEW MEXICO.—HIDALGO COUNTY: Rodeo, 2 Sep 73, *H. annuus*, 1130–1459, 2♀N (EGL, JML).

Subspecies *X. c. diamesa*, which occurs in the Peninsular Ranges of cismontane southern California northward through the Central Coast Ranges into Monterrey County, California, and southward into the Peninsular Ranges of northwestern Baja California (Hurd, 1954), has been taken as follows:

CALIFORNIA.—LOS ANGELES COUNTY: Gorman, 29 Aug 76, *H. annuus*, 0800–0830, 1♀N (AEM, MMM).

The nominate subspecies, which occurs in the North Coast ranges and Sierra Nevada Mountains of California and the southern Cascade Mountains of Oregon (Hurd and Moure, 1963; Hurd, 1978), visits many kinds of flowers for nectar and pollen, but has not been found at those of *Helianthus*.

Smith and Whitford (1978) have recently discussed the factors affecting the nesting success of *X. c. arizonensis* including pollen sources utilized by this subspecies in Arizona, New Mexico, and Mexico (Chihuahua).

Family APIDAE

Members of this family are present throughout much of the world from the high Arctic latitudes to or near the southern limits of the major land masses of the Southern Hemisphere. In America north of Mexico there are 47 species most conspicuously represented by the introduced European honeybee, *Apis mellifera*, and many native species of bumblebees (*Bombus* and *Psithyrus*).

Twenty-five species of this family have been associated with the flowers of *Helianthus* in Amer-

ica north of Mexico. All except four species of the social parasitic genus *Psithyrus* are pollen-collecting species and are either casual polyleges (15 species) or regular polyleges (6 species) of sunflowers.

Genus *Bombus* Latreille

This is a widespread genus that occurs on both the North and South American continents and Eurasia (including Japan and Taiwan, the Philippine Islands, and Indonesia east to Java) and is adventive in New Zealand. Almost half of the species present in America north of Mexico have been found at the flowers of *Helianthus* and doubtless additional species will be found to visit these flowers. Of the 20 species thus far taken at sunflowers most are casual polyleges (14 species), although a surprising number (6 species) are regular polyleges of that plant. At times their numbers become so large as to interfere or even dislodge other anthophilous visitors of sunflowers.

1. *Bombus (Bombus) affinis* Cresson

Fye and Medler (1954) have reported workers of this species at flowers of *Helianthus* in Wisconsin and Graenicher (1909) records workers taking pollen from flowers of *H. giganteus* in the same state. The species occurs from Quebec and Ontario south to Georgia and west to the Dakotas and is evidently a casual polylege of *Helianthus*.

2. *Bombus (Bombus) terricola* Kirby

Two subspecies are currently recognized. The nominate subspecies occurs from Nova Scotia to Florida and westward to South Dakota, Montana, and British Columbia. Workers have been recorded from *Helianthus* in Wisconsin by Fye and Medler (1954); Graenicher (1909) reports workers collecting pollen from flowers of *H. strumosus* in the same state. The western subspecies, *B. terricola occidentalis* Greene, ranges from Alaska to northern California, Nevada, and South Dakota and southward into Arizona and New Mexico. Milliron (1971) gives a number of flower records but

sunflower is not included. Our record is based on the form named *nigroscutatus* by Franklin, which is regarded as a synonym of *occidentalis* by Milliron:

CALIFORNIA.—CONTRA COSTA COUNTY: Antioch, 20 Oct 75, *H. annuus*, 0900-0930, 4♂, 1♀N (EGL, JML).

This species appears to be a casual polylege of *Helianthus*.

3. *Bombus (Fraternobombus) fraternus* (Smith)

Bombus fraternus, a species of eastern and central United States (New Jersey to Florida and west to North Dakota, South Dakota, Nebraska, Colorado, and New Mexico) was reported (as *B. scutellaris* Cresson) from flowers of *Helianthus grosseserratus* and *H. divaricatus* in Illinois by Robertson (1894, 1898) and later by him (Robertson, 1929) from flowers of *H. divaricatus* (♀P), *H. grosseserratus* (♂, ♀) and *H. rigidus* (♀N). LaBerge and Webb (1962), in their list of flowers visited in Nebraska, included *H. annuus*, *H. grosseserratus*, *H. petiolaris*, and *H. rigidus*. The species appears to be a regular polylege of *Helianthus*.

4. *Bombus (Bombias) nevadensis* Cresson

Bombus nevadensis auricomus (Robertson) was recorded from flowers of *Helianthus grosseserratus* and *H. tuberosus* in Illinois by Robertson (1929). According to LaBerge and Webb (1962), this subspecies, which occurs from Ontario to Florida and west to Texas, Oklahoma, Colorado, Wyoming, Montana, and southwestern Canada (Saskatchewan, Alberta, and British Columbia), has been collected often in Nebraska from sunflowers, including *Helianthus annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, and *H. rigidus*.

The nominate subspecies is found from Alaska south to California, Arizona, and New Mexico and east to Wisconsin; it has also been reported from Mexico (Hidalgo). Moldenke and Neff (1974) list four workers of the nominate subspecies from *Helianthus* in California.

The species appears to be a regular polylege of *Helianthus*.

5. *Bombus (Separatobombus) griseocollis* (Degeer)

This species, which ranges across Canada and most of the United States, is regarded by LaBerge and Webb (1962) as having some preference for sunflowers in Nebraska. Among their list of flowers visited are *Helianthus annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, and *H. rigidus*. Earlier, under the name *Bombus separatus* Cresson, Robertson (1894, 1929) had recorded it from *H. annuus*, *H. divaricatus*, *H. grosseserratus*, *H. rigidus*, *H. strumosus*, and *H. tuberosus* in Illinois and Graenicher (1909) reported workers gathering pollen from flowers of *H. giganteus* and *H. strumosus* in Wisconsin. Moldenke and Neff (1974) list 2 queens, 25 workers, and 43 males from *Helianthus* sp. in California. The species appears to be a regular polylege of *Helianthus*.

6. *Bombus (Separatobombus) morrisoni* Cresson

This is a western species ranging from British Columbia to California and east to South Dakota, Nebraska, Colorado, and New Mexico. Titus (1902) first recorded it from *Helianthus annuus* in Colorado. Our collection data appear in Table B and we have also taken it as follows:

CALIFORNIA.—INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0630-0829, 1♂, 40♀P, 10♀N (EGL, JML).

It evidently is a regular polylege of *Helianthus*.

7. *Bombus (Crotchiibombus) crotchii* Cresson

Bombus crotchii occurs in California and Baja California, Mexico. Moldenke and Neff (1974) have recorded 6 males at flowers of *Helianthus*, of which the species may be a casual polylege.

8. *Bombus (Cullumanobombus) rufocinctus* Cresson

Workers and males of *B. rufocinctus* were reported at flowers of *Helianthus* in Wisconsin by Fye and Medler (1954). Possibly this species is a casual polylege of *Helianthus*. It ranges across southern Canada (Nova Scotia, New Brunswick,

and Quebec to British Columbia), across the United States (Maine, Vermont, New York, Michigan, Illinois, Kansas, New Mexico, Arizona, and California), and southward into Mexico (Distrito Federal, Hidalgo, Mexico, Michoacan, Morelos, and Sonora).

9. *Bombus (Pyrobombus) bimaculatus* Cresson

This species, which ranges through most of eastern North America (Ontario and Maine south to Florida and west to Illinois, Kansas, Oklahoma, and Mississippi), has been recorded from *Helianthus* in Nebraska by LaBerge and Webb (1962) and in Wisconsin by Medler and Carney (1963). Robertson (1929) found males visiting the flowers of *H. annuus* in Carlinville, Illinois. It appears to be a casual polylege of *Helianthus*.

10. *Bombus (Pyrobombus) centralis* Cresson

Cockerell (1919) reported a worker from *Helianthus* in Colorado (as *B. justus* Cresson). Moldenke and Neff (1974) listed four workers and five males from *Helianthus* sp. without reference to locality. Graenicher (1909) recorded workers gathering pollen from flowers of *H. strumosus* in Wisconsin. The species ranges from Wisconsin to British Columbia and south to California, Arizona, and New Mexico. It is apparently a casual polylege of *Helianthus*.

11. *Bombus (Pyrobombus) huntii* Greene

This is a western North American species listed by Moldenke and Neff (1974) from *Helianthus* sp. in California. Clements and Long (1923) report it from flowers of *H. petiolaris* in Colorado. The species occurs from British Columbia and Alberta south to California, Nevada, Utah, and New Mexico. It may be a casual polylege of *Helianthus*.

12. *Bombus (Pyrobombus) impatiens* Cresson

A species of eastern North America (Ontario and Maine, south to Florida and west to Michigan, Illinois, Kansas, and Mississippi), *B. impatiens*

has been recorded from *Helianthus annuus* and *H. grosseserratus* in Illinois by Robertson (1929). It appears to be a casual polylege of *Helianthus*.

13. *Bombus (Pyrobombus) ternarius* Say

Fye and Medler (1954) have recorded workers of *B. ternarius* from *Helianthus* in Wisconsin and Graenicher (1909) found workers collecting pollen from flowers of *H. strumosus* in the same state. The species ranges from Yukon east to Nova Scotia and south to Georgia, Michigan, Kansas, Montana, and British Columbia. It appears to be a casual polylege of *Helianthus*.

14. *Bombus (Pyrobombus) vagans vagans* Smith

This nominate subspecies ranges from British Columbia east to Nova Scotia and south to Georgia, Tennessee, South Dakota, Montana, Idaho, and Washington. Workers have been recorded by Graenicher (1909) collecting pollen from flowers of *Helianthus giganteus* and *H. strumosus* in Wisconsin where Fye and Medler (1954) also listed it from *H. sp.*; Robertson (1929) recorded nectar seeking males at flowers of *H. annuus*, *H. grosseserratus*, and *H. tuberosus* in Illinois. With relatively few records of floral visitation available for Nebraska, LaBerge and Webb (1962) could not draw conclusions about floral preferences, but did include *H. annuus* in their list of flowers visited. Workers of this subspecies were recorded (as *B. consimilis* Cresson) from flowers of *Helianthus* in Virginia and Connecticut by Cockerell (1917a). It appears to be a casual polylege of *Helianthus*.

15. *Bombus (Subterraneobombus) appositus* Cresson

Moldenke and Neff (1974) record a worker of this species from *Helianthus* sp. without indication of locality. The species ranges from British Columbia east to Saskatchewan and south to New Mexico, Arizona, and California. It may be a casual polylege of *Helianthus*.

**16. *Bombus (Subterraneobombus) borealis*
Kirby**

A queen of *B. borealis* was recorded from *Helianthus* in Wisconsin by Fye and Medler (1954). The species ranges across southern Canada from Nova Scotia to Alberta and occurs in the northern United States from Maine to New Jersey and west to North Dakota and South Dakota. It may be a casual polylege of *Helianthus*.

**17. *Bombus (Fervidobombus) californicus*
Smith**

One queen and two workers of this western North American species have been listed from *Helianthus* sp. without locality reference by Moldenke and Neff (1974). The species ranges from British Columbia and Alberta in Canada south to California, Arizona, and New Mexico in the United States, and into Mexico (Baja California Norte and Sonora). It is possibly a casual polylege of *Helianthus*.

**18. *Bombus (Fervidobombus) fervidus fervidus*
(Fabricius)**

The nominate subspecies occurs from Quebec and New Brunswick south to Georgia and west to British Columbia, Washington, Oregon, California and into Mexico (Chihuahua). LaBerge and Webb (1962) list the flowers from which this widespread bumblebee has been collected in Nebraska. Included is *Helianthus* sp., but their records do not indicate that sunflower was a preferred host. Cockerell (1919) recorded the species from *H. annuus zonatus* at Falls Church, Virginia, and Moldenke and Neff (1974) from *H. sp.* in California. It appears to be a casual polylege of *Helianthus*.

**19. *Bombus (Fervidobombus) pennsylvanicus pennsylvanicus*
(Degeer)**

This subspecies was recorded at flowers of *Helianthus* by Swenk (1907) and from *H. annuus zonatus* by Cockerell (1917a). Under the name *Bombus americanorum* this bee has been reported at

flowers of *Helianthus annuus*, *H. grosseserratus*, *H. mollis*, *H. rigidus*, *H. tuberosus*, and *H. divaricatus* in Illinois (Robertson, 1894, 1898, 1929), at *H. annuus lenticularis* in Nebraska (Cockerell 1923). LaBerge and Webb (1962) report that in Nebraska it has been most often collected on sunflowers, including *H. annuus*, *H. grosseserratus*, *H. maximiliani*, *H. petiolaris*, and *H. rigidus*. It has also been recorded from sunflowers by Cockerell (1907b) and others. Graenicher (1909) reports nectar-seeking males and workers collecting pollen from flowers of *H. giganteus* and *H. strumosus* in Wisconsin. This subspecies was one of the commonest bees at flowers of *H. annuus* in Austin, Texas, during September 1978. Most workers were seeking nectar as were males and queens, but a few queens and workers occasionally were observed collecting pollen. The principal competing pollen sources were *Solanum elaeagnifolium* and *S. rostratum* which provided nearly all of the pollen collected by this subspecies during these observations. It is evidently a regular polylege of *Helianthus* and ranges from Quebec and Ontario, south to Florida, west to Minnesota, South Dakota, Nebraska, Colorado and New Mexico, and southward into Mexico and possibly Central America.

**20. *Bombus (Fervidobombus) pennsylvanicus sonorus*
Say**

PLATE 5

This subspecies is a frequent visitor to sunflowers in the southwestern United States (Texas west to California) and northwestern Mexico. It was first recorded from this plant in New Mexico by Cockerell and Porter (1899). At times we have found it so numerous at sunflower in Arizona, especially males, as to preclude sampling for other bees. In almost all collections from the southern part of that state this bee was undersampled. It is a regular polylege of *Helianthus*.

Collection records for this subspecies at principal sampling sites may be found in Tables A-E, G, and I-M. In addition it has been taken at sunflowers as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0830–0859, 2♀N (EGL, JML); St. David 1.5 mi W, 3 Sep 61, *H. annuus*, 1♀P (PDH). GRAHAM COUNTY: Franklin, 6 Aug 74, *H. annuus*, 0830–0859, 2♀N (EGL, JML). SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0700–0759, 1♂, 45♀P (EGL, JML), Patagonia 6 mi N, 7 Sep 77, *H. annuus*, 0730–0759, 1♂, 4♀P, 2♀N (EGL, JML).

CALIFORNIA.—CONTRA COSTA COUNTY: Antioch, 21 Sep 75, *H. annuus*, 0900–0930, 4♀N (EGL, JML). FRESNO COUNTY: Parlier, 7 Oct 75, *H. annuus*, 1400–1429, 2♂ (EGL, JML, AEM, MMM). INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0630–0659, 1♀P (EGL, JML). LOS ANGELES COUNTY: Calabasas, 29 Sep 75, *H. annuus*, 0915–0929, 1♀N (AEM, MMM). ORANGE COUNTY: Newport Beach, 27 Aug 76, *H. annuus*, 1400–1429, 5♀P, 15♀N (AEM, MMM). STANISLAUS COUNTY: Ceres, 27 Jul 77, *H. annuus*, 0800–0829, 1♀P (EGL, JML, AEM, MMM); Modesto, 3 Oct 75, *H. annuus*, 0745–0814, 8♂, 2♀N (EGL, JML, AEM, MMM). TULARE COUNTY: Dinuba 5.5 mi S, 7 Oct 75, *H. annuus*, 1200–1229, 4♂, (EGL, JML, AEM, MMM).

Genus *Psithyrus* Lepeletier

Included in this genus are social parasites that live in the nests of the pollen-collecting bumblebees. Four of the six Nearctic species have been taken sipping nectar at the flowers of *Helianthus*, often in company with the species in whose nests they live.

21. *Psithyrus ashtoni* (Cresson)

This species, which occurs across southern Canada (Prince Edward Island west to Saskatchewan) and much of the more northern parts of the eastern United States (North Dakota, Minnesota, Wisconsin, Michigan, Ohio, West Virginia, and Virginia), is a social parasite of *Bombus affinis* and *B. terricola*, both of which are casual polyleges of *Helianthus*. It has been recorded at the flowers of *Helianthus* in Wisconsin by Medler and Carney (1963).

22. *Psithyrus citrinus* (Smith)

Under the name *Psithyrus laboriosus* (Fabricius) (see Mitchell, 1962, for synonymy), Medler and Carney (1963) have recorded females of this species at *Helianthus* in Wisconsin. Earlier, Graenicher (1909) reported the male at *H. strumosus*

from the same state. It is known to be a social parasite in the nests of *Bombus impatiens*, *B. nevadensis auricomus*, and *B. vagans*, all of which visit the flowers of *Helianthus*. It also occasionally attempts to invade hives of the common honeybee, *Apis mellifera* (Hurd, 1979). The species ranges from Prince Edward Island and New Brunswick south to Florida and Alabama and west to South Dakota and North Dakota.

23. *Psithyrus insularis* (Smith)

A widespread North American species listed from *Helianthus* sp. in California by Moldenke and Neff (1974), the species ranges from Canada south to California, Arizona, New Mexico, Nebraska, New York, and New Hampshire. It is known to live as a social parasite in the nests of many species of *Bombus* (Hurd, 1979), including a number of those that also visit flowers of *Helianthus*.

24. *Psithyrus variabilis* (Cresson)

This is a primarily eastern North American species that is parasitic on *Bombus pennsylvanicus* (Frison, 1916, 1921). Robertson (1929) recorded it from *H. annuus* (♂, ♀) and *H. grosseserratus* (♂, ♀, frequent) in Illinois and LaBerge and Webb (1962) included among the flowers visited by this bee in Nebraska, *Helianthus annuus*, *H. grosseserratus*, *H. petiolaris*, and *H. rigidus*. The species ranges from Ohio south to Florida and west to North Dakota, South Dakota, Nebraska, Oklahoma, Texas, New Mexico, and Mexico.

Genus *Apis* Linnaeus

This genus, which is native to Eurasia and Africa, is well established in the Western Hemisphere, having been originally introduced into both North and South America from Europe. While there is much variation evident in the introduced species owing to hybridization of the several introduced races or strains, only one species is represented.

25. *Apis mellifera* Linnaeus

PLATE 5

Honeybees, as the most universally distributed and polylectic of pollinators of agricultural and ornamental crops, as well as entomophilous plants in general, are obviously of special interest to students of sunflower pollination. We have devoted a section to the conflicting information on the role of honeybees in the pollination of commercial sunflowers in the introductory section of this paper (page 19). The data presented here relate to its role in the pollination of wild sunflowers. Unfortunately, it is no more clear-cut or definitive than the data regarding the role of honeybees in the pollination of commercial varieties of sunflower in the United States. This is obviously a subject for more intensive investigation.

Perhaps the strongest statement regarding the role of the honeybee is that of Robertson (1922) in a special situation, at his home in Carlinville, Illinois. He reported that of 153 individuals taken in his yard on *H. annuus* in 1917, *Apis* showed 40.5 percent and of 467 individuals taken on *H. annuus* and *H. divaricatus*, it showed 14.1 percent. Although this can hardly be considered a typical "wild" environment for these species, it is nevertheless significant. Later, he provided summary statistics over the years (Robertson, 1929) for seven local species near Carlinville as follows: *H. annuus* (collections made from cultivated sunflower between 11 July and 6 September yielded 434 specimens of insect visitors, of which 65 were honeybees), *H. divaricatus* (honeybees were present among 53 species of bees collected between 22 July and 10 September—numbers were not given; on 27 August, of 10 species of bees represented by 35 individuals, only one was a honeybee). At *H. grosseserratus*, however, among 72 species of visitors observed between 27 August and 15 October, honeybees were "abundant." On *H. rigidus*, *H. mollis*, *H. scaberrimus*, and *H. tuberosus* during the summer months he found no honeybees.

In his extensive surveys of Wisconsin bees,

Graenicher (1909) reported (without numerical data) worker honeybees taking pollen from *H. giganteus* and nectar and pollen from *H. strumosus*. In his list of sunflower bees at Sterling, Colorado, Cockerell (1911) included no honeybees, at Falls Church, Virginia (Cockerell, 1917a) only one worker, and no *Apis* at Colebrook, Connecticut.

In Orange County, California, Cockerell (1916a) found no honeybees visiting the flowers of *Helianthus lenticularis*, although seven species of native bees were collected and honeybees were present in the vicinity. During a series of surveys of bees and other visitors to *Helianthus annuus* (both wild and commercial varieties) in the central and lower San Joaquin Valley and Delta region of California (particularly Contra Costa, San Joaquin, Stanislaus, Merced, and Madera counties) in the last week of July 1977, we were impressed with the relatively small numbers of honeybees at the flowers in comparison with such native species as *Diadasia enavata*, *Svastra obliqua*, and *Melissodes agilis* (e.g., see Tables I, J, L, M). These last three species were busily taking nectar and pollen, sometimes in incredibly large numbers, yet in half-hour spot samples in a number of localities and all-day samples at three wild sunflower sites involving four collectors, not a single pollen-collecting honeybee was captured or seen. The nectar-gatherers were few, even when a large stand of *H. annuus* in excellent bloom and producing an abundance of pollen and nectar attracting other species of bees was growing within 50 yards of an apiary comprising approximately 25 colonies. Even when taking nectar, the honeybees frequently did not enter the flower head but rested on the large peripheral ray florets and probed the nectar bearing florets from the outside.

The sampling of commercial sunflowers was superficial and largely limited to the periphery of the fields due to the density of the planting, the size of the flowers and the drooping heads, so the relatively small number of honeybees observed in these plantings may have been quite misleading. Large nesting sites, however, of *Svastra obliqua* and *Diadasia enavata* on the edge of one commercial

field from which the females were actively returning with heavy loads of pollen left no doubt that these species can be an important factor in sunflower seed production.

Data from collections at primary survey sites are presented in Tables G, I, J, L, and M. In addition we have taken honeybees at sunflowers as follows:

ARIZONA.—COCHISE COUNTY: Cochise, 8 Sep 75, *H. annuus*, 0800–0859, 1♂P, 5♀N (EGL, JML). PIMA COUNTY: Rillito, 5 mi W, 27 Jun 74, *H. annuus*, 0900–0929, 1♂P (AEM, MMM), 30 Jul 75, *H. annuus*, 1315–1329, 1♀N (AEM, MMM). SANTA CRUZ COUNTY: Nogales, 15 Sep 77, *H. annuus*, 0830–0859, 2♂P, 2♀N, 1600–1629, 1♀P (EGL, JML).

CALIFORNIA.—CONTRA COSTA COUNTY: Antioch, 20 Oct 75, *H. annuus*, 0900–0930, 2♀N (EGL, JML); Byron 4 mi

E, 21 Jul 77, *H. annuus*, 0800–0829, 1♀N (EGL, JML, AEM, MMM). IMPERIAL COUNTY: Holtville 3 mi W, 29 Jul 75, *H. annuus*, 1100–1114, 1♀N (AEM, MMM). INYO COUNTY: Big Pine, 28 Aug 77, *H. annuus*, 0630–0759, 5♂P, 3♀N (EGL, JML). MERCED COUNTY: Atwater, 23 Jul 77, *H. annuus*, 1200–1229, 1♂P, 2♀N (EGL, JML, AEM, MMM). RIVERSIDE COUNTY: Coachella, 8 Jun 76, *H. annuus*, 0900–0929, 1♀N (EGL, JML). SAN DIEGO COUNTY: Highway 8 at Laguna Junction, 13 Jun 74, *H. annuus*, 1300–1415, 1♀N (AEM, MMM). SAN JOAQUIN COUNTY: Manteca 7.5 mi N, 27 Jul 77, *H. annuus*, 1100–1129, 3♂P, 2♀N (EGL, JML, AEM, MMM); Victoria Island, 0.5 mi E of Old River, 0930–0959, *H. annuus* (commercial sunflower), 0930–0959, 1♂P, 1♀N (EGL, JML, AEM, MMM). STANISLAUS COUNTY: Modesto, 3 Oct 75, *H. annuus*, 0745–0815, 1♂P, 2♀N (EGL, JML); Modesto 10 mi S, 27 Jul 77, *H. annuus*, 0800–0829, 2♂P (EGL, JML).

TEXAS.—TRAVIS COUNTY: Austin, 18 Sep 78, *H. annuus*, 0900–1730, 17♂P, 33♀N (PDH).

Appendix

Tables

(For explanation of format, see "Sampling Procedures" in text)

TABLE A.—Silver City, 8 km NW, Grant County, New Mexico, 1798 m elevation; half-hour samples of principal species of bees visiting *Helianthus petiolaris*, 11–12 September 1974 (sky broken with scattered clouds, rain in late afternoon; collectors: E. G. and J. M. Linsley)

Species		0730	0800	0830	0900	0930	1000	1230	1300	1430	1500	1530	Sub-totals	Totals	% of total sample
		0759	0829	0859	0929	0959	1029	1259	1329	1459	1559	1559			
<i>Melissodes agilis</i>	♀P	-	-	-	-	-	-	-	-	-	-	-	0		
	♀N	-	-	-	-	-	*	-	*	1	2	-	3	9	5.2
	♂	1	-	-	2	1	-	2	-	-	-	-	6		
<i>Melissodes montana</i>	♀P	-	3	-	4	3	-	-	-	-	-	2	12		
	♀N	-	-	-	-	1	*	-	*	-	-	-	1	15	8.6
	♂	-	-	-	-	-	-	-	-	-	1	1	2		
<i>Melissodes sonorensis</i>	♀P	-	4	-	-	2	-	-	-	-	-	-	6		
	♀N	-	-	-	-	3	*	-	*	-	-	-	3	9	5.2
	♂	-	-	-	-	-	-	-	-	-	-	-	0		
<i>Melissodes menuachus</i>	♀P	-	-	-	-	1	-	1	-	-	-	-	2		
	♀N	-	-	-	-	-	*	-	*	-	-	-	0	5	2.9
	♂	-	-	-	-	1	-	-	-	-	-	2	3		
<i>Soastra obliqua</i>	♀P	-	-	-	1	-	-	1	-	1	1	-	4		
	♀N	-	-	-	-	-	*	-	*	-	-	-	0	5	2.9
	♂	-	-	-	-	-	-	-	-	1	-	-	1		
<i>Soastra machaerantherae</i>	♀P	-	-	-	-	-	-	1	-	-	-	-	1		
	♀N	-	-	-	-	-	*	-	*	1	-	-	1	3	1.7
	♂	-	-	-	-	-	-	-	-	1	-	-	1		
<i>Syntrichalonia exquisita</i>	♀P	-	-	-	1	-	-	-	-	1	2	-	4		
	♀N	-	-	-	-	-	*	-	*	-	-	-	0	5	2.9
	♂	-	-	-	-	1	-	-	-	-	-	-	1		
<i>Megachile agustini</i>	♀P	1	-	2	1	-	-	1	-	-	1	1	7		
	♀N	-	-	1	-	2	*	-	*	-	1	-	4	13	7.4
	♂	-	-	-	-	1	-	1	-	-	-	-	2		
<i>Megachile inimica</i>	♀P	1	2	-	13	10	-	3	-	4	5	2	40		
	♀N	-	-	-	2	7	*	3	*	1	3	3	19	61	35.1
	♂	-	-	-	-	1	-	1	-	-	-	-	2		
<i>Megachile parallela</i>	♀P	-	-	3	5	-	-	-	-	3	2	2	15		
	♀N	-	-	-	2	-	*	3	*	2	1	-	8	23	13.2
	♂	-	-	-	-	-	-	-	-	-	-	-	0		
Miscellaneous species (16) ¹	♀P	3	-	5	2	1	-	1	-	-	-	-	12		
	♀N	1	-	1	1	4	*	1	*	-	-	-	8	26	14.9
	♂	-	-	-	-	3	-	-	-	1	1	1	6		
Totals		7	9	12	34	42	*	19	*	17	20	14	174	174	100.0

¹ Miscellaneous species: *Andrena accepta* (3♀P), *Andrena helianthi* (2♀P, 1♀N), *Andrena pecosana* (1♀P), *Anthophora curta* (2♀N), *Bombus pennsylvanicus sonorinus* (1♂), *Dufourea marginata* (1♀P, 1♀N), *Halictus ligatus* (1♀P), *Megachile manifesta* (1♂), *Megachile pollicaris* (1♀N), *Melissodes tristis* (1♂), *Nomia micheneri* (2♀P), *Perdita verbesinae* (2♂), *Pseudopanurgus aethiops* (1♀P), *Pterosarus helianthi* (1♀P, 1♀N), *Tripeolus* sp. (2♀N), *Xenoglossodes* sp. (1♂).

TABLE B.—Animas, Hidalgo County, New Mexico, 1341 m elevation, half-hour samples of principal species of bees visiting *Helianthus annuus*, 4–5 September 1974 (sky clear throughout morning, scattered clouds in afternoon; collectors: E. G. and J. M. Linsley)

Species	0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800	1830	Sub-totals	Totals	% of total sample	
<i>Melissodes agilis</i>	2	8	22	15	7	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	5	5	9	7	87	8	215	19.6
♂	-	-	6	2	2	5	9	11	3	5	10	4	5	7	2	3	1	2	4	13	3	4	8	6	5	120	0	13	1.2	
<i>Melissodes montana</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0	10	0.5	
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	0	6	0.5	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	
<i>Melissodes paroselae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	19	1.7	
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	19	1.7	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19	19	230	21.0	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	210	2	10	1.4	
<i>Bombus morrisi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	10	1.4	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	10	1.4	
<i>Bombus pennsylvanicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	19	21	1.9	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	
<i>Andrena accepta</i>	-	-	1	5	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	1	16	1.5	
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3	1.5	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3	1.5	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3	1.5	
<i>Megachile parvella</i>	-	-	4	4	7	6	4	6	2	5	1	2	2	2	2	4	9	9	9	12	8	9	12	11	9	152	61	235	21.5	
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	152	61	235	21.5	
♀N	-	-	2	3	1	1	2	3	4	4	1	4	3	3	3	2	3	2	3	5	2	6	1	1	1	2	22	22	22	21.5
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	22	22	21.5	
<i>Megachile policans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	18	1.6	
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	18	1.6	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	18	1.6	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	18	1.6	

TABLE B—Continued

Species	0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800	1830	Sub-totals	Totals	% of total sample
	17	18	19	21	23	24.5	26	27	28	29	29.5	31	31.5	32	33	33.5	32	33	33.5	32	33	31.5	32	31	31	30			
<i>Swastria macharrantherae</i>			2	4	4	4	8	4	3			1	1						1	2			1				36		
♂						1	1	1	1				2							2							8		
♀			2	1	1	2	1	1	2	1	2	3	2	6	2	4	4	1	1	4	1	1	3	3	1	1	50	94	8.6
<i>Swastria obliqua</i>					3	3	2	3	1										1	1	1	1	1	1	2	1	21		
♂																					1	1	2	1	1	1	5	42	3.8
♀								1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	16		
<i>Swastria sita</i>																											0		
♂																											4	24	2.2
<i>Pseudopanurgus aethiops</i>																											20		
♂																											4		
♀																											1	26	2.4
<i>Falictus ligatus</i>																											21		
♂																											7		
♀																											2	12	1.1
<i>Agapostemon angelicus</i>																											3		
♂																											0	17	1.6
<i>Coelioxys edita</i>																											16		
♂																											0		
♀																											10	24	2.2
<i>Tripoeolus spp. (3)</i>																											0		
♂																											10	25	2.3
♀																											15		
Miscellaneous species (23) ¹																											5	43	3.9
Totals	4	9	38	46	39	26	45	36	31	40	49	61	60	61	36	44	50	40	38	63	46	45	33	46	40	26	1095	1095	100.0

¹ Miscellaneous species: *Anthidium maculosum* (1♂), *Anthidium porterae* (2♀), *Anthophora curta* (1♀, 1♀, 1♂), *Anthophora montana* (3♀), *Anthophora smithii* (1♂), *Diadasia ochracea* (2♂), *Dufourea marginata* (1♀), *Megachile brevis* (1♂), *Megachile inimica* (2♂), *Megachile sidalceae* (2♂), *Megachile texana* (1♂), *Melissodes brevipennis* (1♀), *Melissodes humilior* (1♀), *Melissodes limbatus* (3♂), *Melissodes menachus* (1♂), *Melissodes subagitis* (3♂), *Melissodes submenucha* (5♂), *Melissodes thelypodii* (1♀), *Melissodes verbesinarum* (2♂), *Nomada* sp. (1♂), *Nomia heteropoda* (1♀), *Nomia sabinensis* (1♀, 1♀, 2♂), *Xrometeia interrupta* (1♀); data for miscellaneous species not recorded by time periods.

	20	80	101	88	70	76	124	155	117	83	78	85	86	78	89	74	42	44	43	33	105	108	101	67	12	1959	1959	100.0	
<i>Melissodes montana</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	
♂N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	28	1.4	
♂	-	-	-	1	-	-	3	8	-	-	-	1	1	1	-	-	-	3	-	-	-	-	-	-	-	21	-	-	
<i>Tripeolus</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
♀N	-	-	-	-	1	-	4	6	4	6	2	7	7	2	8	4	7	6	2	4	13	8	-	-	-	92	110	5.6	
♂	-	-	-	-	-	-	-	-	3	1	1	-	-	1	1	1	1	1	5	-	1	-	2	-	-	18	-	-	
<i>Tripeolus norae</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
♀N	-	-	-	-	2	2	4	1	1	2	-	2	1	1	-	-	-	1	1	-	1	-	-	-	-	19	22	1.1	
♂	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	3	-	-	
<i>Megachile inimica</i> ♀P	-	-	-	-	1	-	3	2	1	3	1	-	-	1	-	2	1	-	-	1	2	1	-	-	-	19	-	-	
♀N	-	-	-	-	-	1	7	5	12	4	3	3	-	2	3	3	-	-	-	1	1	-	-	-	-	45	66	3.4	
♂	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
<i>Xeromelicta interrupta</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
♀N	-	-	-	-	1	1	-	2	1	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	0	8	9	0.5
♂	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Melissodes tristis</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	3	-	-	-	5	10	0.5	
♀N	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	10	0.5	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
<i>Megachile montivaga</i> ♀P	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3	14	0.7	
♂	-	-	-	-	-	-	2	1	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	9	-	-	
<i>Agapostemon hyeri</i> ♀P	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	8	0.4	
♂	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	
<i>Melissodes coreopsis</i> ♀P	-	-	-	-	-	1	1	1	1	1	-	-	-	1	2	1	-	1	-	2	-	-	-	-	-	11	17	0.9	
♀N	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	
♂	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
<i>Swastra pretulca suffusa</i> ♀P	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	0.3	
♀N	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	0.3	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
<i>Megachile politaris</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
♀N	-	-	-	-	-	-	-	-	-	2	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	5	18	0.9	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	
<i>Anthidium maculosum</i> ♀P	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
♀N	-	-	-	-	-	-	1	-	-	-	-	-	-	2	1	2	-	-	-	-	-	-	-	-	-	8	20	1.0	
♂	-	-	-	-	-	-	2	-	-	-	-	-	2	2	4	-	-	-	-	-	2	-	-	-	-	12	-	-	
<i>Centris atripes</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	14	0.7	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	
<i>Heteranthidium cordaticeps</i> ♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	11	0.5	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	
<i>Miscellaneaous</i> ♀P	-	-	4	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	
♀N	-	-	1	-	2	1	4	1	2	1	4	-	-	-	-	-	-	-	-	-	1	1	-	-	-	21	51	2.6	
♂	-	-	2	-	2	-	3	2	1	1	1	-	-	2	1	1	1	1	1	1	1	1	1	1	1	21	-	-	

Totals 20 80 101 88 70 76 124 155 117 83 78 85 86 78 89 74 42 44 43 33 105 108 101 67 12 1959 1959 100.0

¹ Miscellaneous species: *Anthidium porterae* (1♀N, 3♂), *Anthophora urbana* (1♀N, 1♂), *Centris caesalpiniae* (1♀N), *Chalcidoma occidentalis* (1♀N), *Coelioxys edita* (4♀, 1♂), *Coelioxys menthae* (1♂), *Colletes rufocinctus* (1♀N), *Colletes uvotomi* (1♀N), *Diadotia ochracea* (1♀N), *Diadotia pruinosiformis* (3♀P, 1♀N), *Diadotia sp.* (2♀P), *Exomalopsis solani* (1♀N), *Exomalopsis solidaginis* (1♀N), *Melissodes confusa* (2♂), *Melissodes memachus* (3♂), *Nomada sp.* (2♀), *Paramonada velutina* (1♀N), *Perditia linguatilis* (1♀P, 2♂), *Swastra helianthelli* (2♀P, 1♂), *Swastra texana elata* (1♀P, 2♂), *Syrinchalonia exquisita* (1♂), *Tripeolus trichopygus* (1♀, 1♂), *Xenoglossodes erocorphi* (1♂), *Xenoglossodes sp.* (1♀N, 1♂), *Xylacopa californica arizonensis* (2♀N). Nectar-drinking males of *Bombus pennsylvanicus sonorus* were present in numbers (±300) throughout the day, but were not sampled, and therefore are excluded from the table. Pollen-gathering females (workers) were scarce (±25). No honey bees were present.

TABLE D.—Double Adobe, Cochise County, Arizona; half-hour samples of principal species of bees visiting *Helianthus annuus* on various dates in 1974 and 1975 (collectors: P. D. Hurd, Jr., A. E. and M. M. Michelbacher, E. G. and J. M. Linsley)

Species		0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1300	1330	1400	1430	1500	1530	1600	1630	Sub-totals	Totals	% of total sample
		0629 18	0659 19	0729 20	0759 21	0829 23	0859 25	0929	0959	1029	1259	1329	1359	1429	1459	1529	1559	1629	1659			
<i>Bombus pennsylvanicus sonorus</i>	♀P	-	1	1	2	2	-	1	2	-	-	1	3	2	1	-	2	-	18	33	54	8.9
	♀N	-	-	1	2	10	2	3	-	3	*	8	-	1	-	1	-	2				
	♂	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-				
<i>Melissodes agilis</i>	♀P	-	2	1	7	20	5	-	-	-	-	1	-	-	-	-	1	2	15	157	25.7	
	♀N	-	-	-	2	-	-	-	2	-	*	3	2	2	1	3	-	-				
	♂	-	-	2	1	25	1	-	-	-	-	16	8	10	12	18	10	-				
<i>Halictus ligatus</i>	♀P	-	2	15	20	35	8	-	-	-	-	1	-	-	-	2	3	1	13	102	16.7	
	♀N	-	-	-	1	3	8	-	-	-	*	-	-	-	-	-	-	1				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-				
<i>Dialictus pruinosiformis</i>	♀P	-	-	17	25	17	6	4	-	-	-	-	-	-	1	3	1	-	22	96	15.7	
	♀N	-	-	2	5	6	2	1	-	-	*	-	-	-	-	2	2	2				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Agapostemon angelicus</i>	♀P	-	-	11	3	2	1	-	-	-	-	-	-	-	-	1	3	2	3	31	5.1	
	♀N	-	-	-	1	1	-	-	-	-	*	-	-	-	-	-	-	1				
	♂	-	-	-	-	1	-	-	-	-	1	1	2	-	-	-	-	-				
<i>Megachile parallela</i>	♀P	-	-	-	2	4	5	2	2	-	-	2	-	-	1	-	2	3	1	8	32	5.2
	♀N	-	-	1	-	3	2	-	-	-	*	1	-	1	-	-	-	-				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Pseudopanurgus aethiops</i>	♀P	-	-	-	1	1	-	-	-	2	-	1	-	-	-	-	-	-	2	22	3.6	
	♀N	-	-	-	-	1	-	-	-	-	*	1	-	-	-	-	-	-				
	♂	-	-	-	1	1	-	2	1	-	-	2	-	1	-	7	-	-				
<i>Nomia heteropoda</i>	♀P	-	-	-	1	-	1	-	-	-	-	1	-	1	-	-	-	-	0	7	1.1	
	♀N	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-				
	♂	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-	-				
<i>Soastra machaerantherae</i>	♀P	-	-	-	-	2	3	2	-	-	-	1	-	-	-	-	-	-	29	47	7.7	
	♀N	-	-	-	-	13	10	6	-	-	*	-	-	-	-	-	-	-				
	♂	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	7	-				
<i>Perdita albipennis</i>	♀P	-	-	-	-	1	2	-	-	-	-	2	2	-	1	2	-	2	0	12	2.0	
	♀N	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Apis mellifera</i>	♀P	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	5	0.8	
	♀N	-	-	-	-	2	1	1	-	-	*	-	-	-	-	-	-	-				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Triepolus</i> sp.	♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	9	1.5	
	♀N	-	-	-	-	-	-	-	-	-	*	1	-	3	-	1	-	-				
	♂	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-				
Miscellaneous species (21) ¹	♀P	-	-	-	1	1	1	-	-	-	-	4	-	-	-	2	1	-	6	36	6.0	
	♀N	-	-	-	2	1	-	-	-	-	-	1	-	-	-	1	1	-				
	♂	-	-	-	-	5	3	-	-	-	-	6	-	-	-	4	2	-				
Totals		0	5	51	79	159	61	22	9	6	*	8	53	23	18	19	54	31	12	610	610	100.0

¹ Miscellaneous species: *Agapostemon cockerelli* (1♀P), *Andrena accepta* (2♀P), *Anthidium porterae* (1♂), *Ashmeadiella californica* (1♂), *Colletes perileucus* (1♀N), *Colletes wootoni* (1♂), *Duadasia diminuta* (1♂), *Exomalopsis solani* (3♀P), *Megachile agustini* (2♀N, 1♂), *Megachile gentilis* (1♀N), *Megachile mendica snowi* (1♂), *Melissodes composita* (1♀P), *Melissodes menuachus* (1♂), *Melissodes montana* (1♀P), *Melissodes paroselae* (2♂), *Melissodes subagilis* (1♀N), *Melissodes tristis* (6♂), *Protandrena mexicanorum* (1♂), *Soastra obliqua* (1♀P, 2♂), *Soastra texana ebata* (1♀P, 2♂), *Xenoglossodes* sp. (1♀N).

TABLE E.—Benson, Cochise County, Arizona, 1091 m elevation; half-hour samples of principal species of bees visiting *Helianthus annuus*, 14 September 1974 (sky broken, scattered clouds beginning about 1100, rain at about 1430; collectors: E. G. and J. M. Linsley)

Species		0700	0730	0800	0830	0900	0930	1000	1030	1100	1300	1330	1400	Sub-totals	Totals	% of total sample
		0729	0759	0829	0859	0929	0959	1029	1059	1259	1329	1359	1429			
		19	21	23	25	26	28	29	31		33.5	24	24			
<i>Melissodes agilis</i>	♀P	3	6	16	15	3	—	—	—	—	—	—	—	43	81	38.4
	♀N	—	—	—	—	1	—	—	—	*	—	—	—	1		
	♂	—	—	10	4	5	5	6	—	—	5	—	2	37		
<i>Bombus pennsylvanicus sonorus</i>	♀P	—	—	1	—	2	—	—	—	—	—	—	1	4	13	6.7
	♀N	1	1	—	1	3	—	—	—	*	1	1	1	9		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	0		
<i>Pseudopanurgus aethiops</i>	♀P	—	—	6	2	1	—	—	—	—	—	—	—	9	35	16.7
	♀N	—	—	2	1	—	1	—	—	*	—	—	—	4		
	♂	—	—	6	8	2	4	1	—	—	—	—	1	22		
<i>Pterosarus helianthi</i>	♀P	—	—	—	—	1	—	—	—	—	—	—	—	1	5	2.4
	♀N	—	—	—	—	1	—	—	—	*	—	—	—	1		
	♂	—	—	—	1	2	—	—	—	—	—	—	—	3		
<i>Andrena accepta</i>	♀P	—	—	1	2	1	1	1	—	—	—	—	—	6	6	2.8
	♀N	—	—	—	—	—	—	—	—	*	—	—	—	0		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	0		
<i>Halictus ligatus</i>	♀P	—	—	2	1	4	1	—	—	—	—	—	—	8	16	7.6
	♀N	—	—	1	—	1	1	2	—	*	1	1	—	7		
	♂	—	—	—	—	—	—	1	—	—	—	—	—	1		
<i>Melissodes tristis</i>	♀P	—	—	—	—	—	—	—	—	—	—	—	—	0	28	13.3
	♀N	—	—	—	—	—	—	—	—	*	—	—	—	0		
	♂	—	—	—	—	3	6	—	1	—	1	9	8	28		
Miscellaneous species (16) ¹	♀P	—	—	1	1	—	—	—	2	—	—	—	—	4	27	12.8
	♀N	—	—	—	—	1	1	1	1	*	1	—	—	5		
	♂	—	—	1	1	3	4	—	5	—	3	—	1	18		
Totals		4	7	47	37	34	24	12	9	*	12	11	14	211	211	100.0

¹ Miscellaneous species: *Agapostemon angelicus* (1♂), *Agapostemon cockerelli* (1♀N, 2♂), *Agapostemon melliventris* (1♀N), *Dialictus clematisellus* (1♀N), *Dialictus microlepoides* (1♀N, 1♂), *Dialictus oleosus* (1♂), *Dialictus* sp. (1♂), *Dufourea marginata* (4♂), *Evylaeus amicus* (1♂), *Evylaeus pectoraloides* (1♀N), *Melissodes coreopsis* (2♀P), *Melissodes menuachus* (2♀P), *Melissodes montana* (1♂), *Melissodes paroselae* (2♂), *Melissodes submenuacha* (2♂), *Perdita verbesinae* (2♂).

TABLE F.—Indio, Riverside County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 18 September 1977 (pollen essentially all removed by bees by midmorning, small amount available at midafternoon; collectors: E. G. and J. M. Linsley)

Species		0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1400	1430	1500	1530	1600	Sub- totals	Totals	% of total sample
		0629 23	0659 24.5	0729 26	0759 27	0829 28	0859 28.5	0929 29.5	0959 31	1029 32	1359	1429 33.5	1459 33	1529 33	1559 32	1629 31.5			
<i>Nomia heteropoda</i>	♀P	11	31	14	15	7	6	5	3	2		1	1	1	3	4	104		
	♀N	-	-	-	-	1	2	2	1	2	*	1	-	-	-	-	9	220	43.8
	♂	13	9	12	4	6	5	11	6	7		5	7	10	6	6	107		
<i>Melissodes agilis</i>	♀P	2	2	2	1	2	-	-	-	-		-	-	2	2	1	14		
	♀N	1	-	-	1	-	-	-	-	-	*	-	-	-	1	1	4	229	45.6
	♂	2	8	22	9	10	17	27	21	23		15	14	15	16	12	211		
<i>Halictus ligatus</i>	♀P	-	1	5	1	3	-	-	-	-	-	-	-	-	1	-	11		
	♀N	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	12	2.4
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
<i>Megachile parallela</i>	♀P	1	-	3	1	-	-	-	-	-	-	-	-	1	2	-	8		
	♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	18	3.6
	♂	-	-	-	3	-	-	1	-	1	-	-	1	1	3	-	10		
<i>Apis mellifera</i>	♀P	2	2	5	-	-	-	-	-	-	-	-	-	2	-	-	11		
	♀N	1	-	3	-	-	-	-	-	-	-	-	-	2	-	-	6	18	3.6
	♂	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1		
Miscellaneous species (5) ¹	♀P	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1		
	♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	5	1.0
	♂	-	1	-	-	-	-	1	-	-	-	-	1	-	1	-	4		
Totals		33	54	66	35	29	32	47	31	35	0	22	24	35	35	24	502	502	100.0

¹ Miscellaneous species: *Agapostemon texanus* (1♂), *Chalicodoma occidentalis* (1♀N), *Melissodes robustior* (1♂), *Nomia nevadensis angelesia* (1♀P), *Triepeolus lestes* (1♂).

TABLE G.—Bishop, Inyo County, California, 1292 m elevation; half-hour samples of principal species of bees visiting *Helianthus annuus*, 27 August 1977 (sunrise, 0610; clear in morning, cloudy in afternoon, particularly over Sierra Nevada Mountains in the west; collectors: E. G. and J. M. Linsley)

Species		0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	Sub-totals	Totals	% of total sample
		0629	0659	0729	0759	0829	0859	0929	0959	1029	1059	1129	1159	1229	1259	1329			
<i>Melissodes agilis</i>	♀P	-	-	25	15	16	7	-	1	-	-	-	-	-	-	-	64	178	67.4
	♀N	-	-	-	-	2	-	5	-	2	-	1	-	2	1	-	13		
	♂	-	-	1	4	24	17	14	10	5	3	6	6	5	4	2	101		
<i>Andrena accepta</i>	♀P	-	-	-	2	2	-	1	-	1	-	1	-	-	-	-	7	33	12.5
	♀N	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1		
	♂	-	-	-	-	-	-	-	6	4	7	5	-	2	-	1	25		
<i>Megachile polticaris</i>	♀P	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	2	5	1.9
	♀N	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	2		
	♂	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1		
<i>Diadasia enavata</i>	♀P	-	-	-	-	-	1	1	1	1	-	1	-	1	1	-	7	20	7.6
	♀N	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1		
	♂	-	-	-	-	3	1	2	2	-	-	-	2	-	1	1	12		
<i>Bombus pennsylvanicus sonorus</i>	♀P	-	-	-	-	-	-	-	1	1	1	1	-	1	-	-	5	9	3.4
	♀N	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	3		
	♂	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1		
<i>Apis mellifera</i>	♀P	-	-	-	1	-	-	-	-	2	2	-	1	-	-	-	6	14	5.3
	♀N	-	-	-	-	-	-	2	2	-	-	-	-	2	1	1	8		
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
Miscellaneous species (4) ¹	♀P	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	2	5	1.9
	♀N	-	-	1	-	-	-	1	-	1	-	-	-	-	-	-	3		
	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
<i>Totals</i>		0	0	27	24	47	26	28	26	20	14	16	9	13	9	5	264	264	100.0

¹ Miscellaneous species: *Anthophora urbana urbana* (2♀N), *Megachile parallela* (1♀P), *Melissodes appressa* (1♀N), *Melissodes lustra* (1♀P). *Melissodes agilis* (15♀, 29♂) sleeping curled together on separate flower heads.

TABLE H.—Corcoran, Kings County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 6 October 1975 (cool breeze in early morning after heavy rain previous evening, sky clear at sunrise but clouds forming by 0930, broken sky and cool breeze until early afternoon, gusty wind and clouds about 1300 and dust storm approaching by late 1400, all activity over; collectors: E. G. and J. M. Linsley and A. E. and M. M. Michelbacher)

Species		0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	Sub-totals	Totals	% of total sample
		0759 12	0829 13	0859 14.5	0929 15	0959 15.5	1029 16	1059 17	1129 19	1159 22	1229 26	1259 29	1329 30.5	1359 29	1429 28			
<i>Melissodes agilis</i>	♀P	-	6	12	4	6	1	4	-	-	-	-	-	-	-	33		
	♀N	-	1	3	2	1	1	-	2	1	1	2	-	-	-	14	54	8.0
	♂	-	-	-	-	1	-	-	-	4	-	1	1	-	-	7		
<i>Diadasia enavata</i>	♀P	-	-	-	1	1	-	-	-	3	1	2	-	-	-	8		
	♀N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	357	52.7
<i>Halictus ligatus</i>	♂	-	-	8	16	30	28	20	30	52	41	52	38	34	-	349		
	♀P	-	-	-	6	7	7	12	10	4	2	-	-	-	-	48		
	♀N	-	-	-	-	1	-	-	-	-	2	3	-	-	-	6	238	35.6
<i>Melissodes lupina</i>	♂	-	-	-	6	16	25	24	20	13	10	21	24	25	-	184		
	♀P	-	-	-	-	-	1	-	-	-	-	-	-	1	-	2		
	♀N	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	11	1.6
<i>Svastra obliqua</i>	♂	-	-	-	-	-	1	3	-	-	2	1	-	-	-	7		
	♀P	-	-	-	-	-	-	-	-	-	1	-	1	-	-	2		
	♀N	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	6	0.9
Miscellaneous species (7) ¹	♂	-	-	-	-	-	-	1	-	1	-	-	1	-	-	3		
	♀P	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2		
	♀N	-	-	-	-	-	-	-	-	1	1	1	1	-	-	4	11	1.6
Totals		0	7	25	35	64	65	64	62	81	61	86	66	61	0	677	677	100.0

¹ Miscellaneous species: *Agapostemon texanus* (1♀P), *Anthophora curta* (2♂), *Anthophora urbana* (1♀N, 2♂), *Dialictus* sp. (1♂), *Halictus confusus* (1♀N), *Lasioglossum* sp. (1♀P, 1♀N), *Triepeolus lineatulus* (1♀N). Sleeping on flower heads: *Diadasia enavata* (38♂), *Halictus ligatus* (3♂), *Melissodes agilis* (1♂).

TABLE I.—Madera, Madera County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 24 July 1977 (sunrise, 0512; sky clear; collectors: E. G. and J. M. Linsley, A. E. and M. M. Michelbacher)

Species	0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	Sub-totals	Totals	% of total sample
<i>Diadasia enavata</i>	89	62	65	49	38	29	37	29	49	46	34	38	27	14	24	13	18	27	37	29	21	20	795	1152	89.1
♀P	7	10	6	9	5	16	4	4	9	11	8	6	2	-	2	2	12	12	5	10	6	7	153		
♂	9	18	20	16	21	10	9	5	9	6	4	6	3	1	1	3	3	13	17	12	8	10	204		
<i>Swastra obliqua</i>	1	-	1	-	1	1	1	-	3	3	5	2	3	4	4	4	3	2	6	5	4	5	58	82	6.3
♀P	1	-	-	-	-	-	-	-	7	1	-	1	1	3	1	1	1	1	1	-	-	-	18		
♂	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	6		
<i>Melissodes agilis</i>	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	4	11	0.9
♀P	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	2		
♂	-	-	-	-	-	2	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	5	5		
<i>Bombus pennsylvanicus</i>	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	9	0.7
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2		
♂	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	2		
<i>Halictus ligatus</i>	1	-	1	-	2	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	7	10	0.8
♀P	-	-	-	1	1	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	2		
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
<i>Apis mellifera</i> (w.)	2	1	1	4	2	-	-	3	-	1	-	1	-	1	2	-	-	1	1	-	-	-	20	20	1.5
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
Miscellaneous species (3) ¹	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	9	0.7
♀P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0		
Totals	107	94	94	76	76	65	54	41	82	68	54	57	38	23	32	27	37	57	67	57	43	44	1293	1293	100.0

¹ Miscellaneous species: *Anthophora urbana* (3♂), *Megachile brevis* (1♀P, 1♂), *Xeromelecta californica* (4♂), *Halictus ligatus* (1♂), *Melissodes agilis* (1♂).

TABLE J.—Madera, Madera County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 21 September 1977 (sunrise behind clouds, 0600; anthesis beginning 0705; collectors: E. G. and J. M. Linsley)

Species		0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1330	1400	1430	1500	1530	1600	Sub-totals	Totals	% of total sample
		0629	0659	0729	0759	0829	0859	0929	0959	1029	1059	1129	1329	1359	1429	1459	1529	1559	1629			
		15	15	14.5	16.5	18	20	21.5	22	23	24	25.5		33	32.5	32	31	30	28			
<i>Diadasia enavata</i>	♀P	-	-	24	45	23	16	5	7	10	6	9		16	18	14	22	16	12	243	590	83.8
	♀N	-	6	1	-	-	-	-	-	-	-	1	*	2	2	3	4	4	1	24		
	♂	-	-	17	19	31	20	24	19	21	26	20		20	19	21	27	20	19	323		
<i>Melissodes agilis</i>	♀P	-	-	2	5	2	2	1	-	-	-	-		-	-	4	1	2	4	23	40	5.7
	♀N	-	1	-	-	-	-	-	1	2	1	-	*	-	-	1	1	-	-	7		
	♂	-	-	2	1	-	1	1	-	1	-	-		-	-	-	1	2	1	10		
<i>Bombus pennsylvanicus sonorus</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	1	-	-	-	-	1	18	2.5
	♀N	-	-	1	-	3	3	-	1	2	-	-	*	-	-	-	-	-	-	10		
	♂	-	-	-	-	-	-	-	1	1	-	-		-	-	2	2	1	-	7		
<i>Anthophora urbana</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0	11	1.6
	♀N	-	-	-	-	-	-	-	-	-	-	-	*	-	-	1	-	-	-	1		
	♂	-	-	1	-	1	-	1	-	1	-	-		1	-	1	1	3	-	10		
<i>Xeromelecta californica</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0	6	0.8
	♀N	-	-	-	-	-	-	-	-	-	-	-	*	-	-	1	-	-	-	1		
	♂	-	-	-	-	-	-	-	1	-	-	-		-	-	1	1	2	-	5		
<i>Melissodes lupina</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	-	2	-	-	-	2	7	1.0
	♀N	-	-	-	-	-	-	-	-	-	-	-	*	-	1	1	2	1	-	5		
	♂	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0		
<i>Swastra obliqua</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	1	1	5	2	3	12	16	2.3
	♀N	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	2	1	1	4		
	♂	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0		
<i>Apis mellifera</i>	♀P	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0	14	2.0
	♀N	-	1	2	1	3	-	1	1	-	1	-	*	-	-	1	-	1	2	14		
	♂	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0		
Miscellaneous species (1) ¹	♀P	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0	1	0.3
	♀N	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	0		
	♂	-	-	-	-	-	-	-	-	-	-	1		-	-	-	-	-	-	1		
Totals		0	8	50	71	63	42	34	30	37	35	31	*	39	42	54	69	55	43	703	703	100.0

¹ Miscellaneous species: *Halictus ligatus* (1♂). Sleeping: *Diadasia enavata* (3♀, 32♂), *Melissodes agilis* (3♂).

TABLE K.—Madera, Madera County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 5 October 1975 (cool morning after cool night, sun generally bright; sunrise, 0540; very little pollen available until after 0700; first bee checking flowers for pollen and/or nectar at 0656; first bee gathering pollen at 0715; collectors: E. G. and J. M. Linsley, A. E. and M. M. Michelbacher)

Species	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	Sub-totals	Totals	% of total sample
<i>Melissodes agilis</i>	2	1	1	2	2	6	1	3	-	-	2	-	1	-	3	4	1	7	5	1	109	186	25.3	
♂	-	1	1	2	2	6	1	3	2	1	1	-	3	-	2	5	12	4	-	-	42	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	-	-	
<i>Bombus pennsylvanicus sonorus</i>	5	6	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	0	35	4.8	
♂	-	1	-	-	1	-	2	4	1	1	1	-	-	-	3	1	4	-	-	-	19	-	-	
♀	7	7	14	7	3	4	5	3	9	1	6	6	3	2	1	2	4	6	4	2	96	182	24.8	
♂	3	2	1	1	2	1	-	1	2	-	-	-	3	-	-	3	3	-	-	-	22	-	-	
♀	-	3	7	2	3	2	2	1	4	-	3	2	5	2	3	3	6	6	5	-	64	-	-	
<i>Agapostemon texanus</i>	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	0.8	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Suastra obliqua</i>	-	5	17	2	9	19	8	6	10	4	4	4	8	4	4	9	4	4	4	5	139	207	28.2	
♂	-	-	-	1	-	3	-	3	6	3	2	1	7	1	2	3	3	2	4	5	47	-	-	
♀	-	-	-	1	1	2	1	-	3	-	-	-	-	-	-	-	1	2	1	3	21	-	-	
<i>Halictus ligatus</i>	-	1	1	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	5	7	1.0	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
<i>Anthophora urbana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	24	3.3	
♂	-	-	2	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	4	-	-	
♀	-	-	1	2	1	2	1	2	1	1	-	-	-	-	1	2	2	-	3	-	20	-	-	
<i>Melissodes lupina</i>	-	-	3	4	1	1	-	3	1	1	1	1	1	-	-	1	2	-	-	-	20	65	8.9	
♂	-	-	1	4	-	2	2	2	2	6	6	3	5	1	1	1	1	2	4	-	44	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Tripeolus lineatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	5	0.7	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Melissodes robustior</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	5	0.7	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
<i>Megachile imitica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	5	0.7	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	
Miscellaneous species (5) ¹	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	7	1.0	
♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	
♀	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	
Totals	32	49	75	38	30	55	27	38	42	22	28	19	41	16	13	32	40	47	36	35	19	734	734	100.0

¹ Miscellaneous species: *Anthophora curva* (2♂), *Chalcidodoma angelarum* (1♀N), *Megachile parviflora* (1♀N, 1♂), *Tripeolus concavus* (2♀N), *T. lineatus* (1♂). Sleeping on flower heads: *Bombus pennsylvanicus sonorus* (3♂, 1♂), *Diadasia enavata* (3♀, 1♂), *Melissodes agilis* (1♀, 5♂), *Suastra obliqua* (1♀, 1♂).

TABLE L.—Merced, Merced County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 4 October 1975 (sunrise, 0605; sunset, 1738; thin clouds in sky but sun generally bright; honey bees searching flowers at 0650 but no new nectar or pollen yet available; first *Melissodes* with pollen at 0715; pollen visibly becoming available by 0730, more so at 0800; collectors: E. G. and J. M. Linsley)

Species		0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1530	1600	Sub-totals	Totals	% of total sample
		0629	0659	0729	0759	0829	0859	0929	0959	1029	1059	1129	1159	1229	1529	1559	1629			
		14	15	16	20	21.5	22.5	24	25.5	26	28	32	34	35		36	35			
<i>Melissodes agilis</i>	♀P	—	—	2	4	2	1	2	1	3	4	—	—	—	—	—	2	21	72	21.3
	♀N	—	—	—	—	1	2	2	1	—	—	—	—	—	*	—	1	7		
	♂	—	—	—	—	5	8	10	9	11	—	—	—	—	—	—	1	44		
<i>Soastra obliqua</i>	♀P	—	—	—	6	7	4	6	10	27	19	16	11	1	—	15	12	134	187	55.3
	♀N	—	—	—	1	—	—	—	—	4	12	10	—	3	*	1	1	32		
	♂	—	—	—	—	—	—	—	—	5	4	4	—	—	—	4	4	21		
<i>Bombus pennsylvanicus sonorus</i>	♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	22	6.5
	♀N	—	—	—	1	1	—	2	1	3	—	2	1	—	*	2	—	13		
	♂	—	—	—	—	1	1	—	—	1	1	—	—	2	—	3	—	9		
<i>Megachile parallela</i>	♀P	—	—	—	—	1	—	2	—	1	—	1	—	—	—	—	—	5	5	1.5
	♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	0		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0		
<i>Diadasia enavata</i>	♀P	—	—	—	—	—	—	—	1	—	—	1	—	—	—	1	—	3	11	3.3
	♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	0		
	♂	—	—	—	—	—	1	—	—	3	1	—	—	—	—	3	—	8		
<i>Halictus ligatus</i>	♀P	—	—	—	—	—	1	2	—	1	—	2	—	—	—	—	—	6	8	2.4
	♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	*	1	1	2		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0		
<i>Melissodes lupina</i>	♀P	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	7	2.1
	♀N	—	—	—	—	—	—	—	1	—	2	—	1	1	*	—	1	6		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0		
<i>Anthophora urbana</i>	♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	7	2.1
	♀N	—	—	—	—	—	—	—	—	—	—	—	—	1	*	—	1	2		
	♂	—	—	—	—	—	—	—	—	—	2	1	2	—	—	—	—	5		
<i>Apis mellifera</i>	♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	19	5.6
	♀N	—	—	1	1	2	1	3	2	2	1	1	2	1	*	—	1	18		
	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0		
Totals		0	0	3	13	20	19	29	26	61	46	38	18	9	*	31	25	338	338	100.0

TABLE M.—Escalon, San Joaquin County, California; half-hour samples of principal species of bees visiting *Helianthus annuus*, 22 July 1977 (sunrise, 0510; sky clear, slight breeze in afternoon; collectors: E. G. and J. M. Linsley, A. E. and M. M. Michelbacher)

Species	Time																				Sub-totals	Totals	% of total sample		
	0600	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530				1600	1630
<i>Diadasia enavata</i>	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	20	12	11	13	4	3	4	9	6	10	12	10	1	2	28	18	16	14	34	22	17	14	18	12
<i>Melissodes agilis</i>	12	25	12	10	7	3	2	—	3	—	—	—	—	1	1	—	2	3	—	2	7	2	3	1	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	4	32	15	16	13	18	5	11	4	1	5	9	29	20	7	4	2	6	5	9	5	2	1	228
<i>Swastra obliqua</i>	2	7	9	18	11	14	8	15	14	9	7	7	6	2	1	22	72	15	12	10	15	8	4	7	301
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	1	—	7	4	5	7	2	5	12	9	12	9	6	12	21	20	11	6	11	20	10	11	11	3
<i>Halictus ligatus</i>	—	4	7	4	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Agapostemon texanus</i>	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Apis mellifera</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	1	2	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Miscellaneous species (8) ¹	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Totals	36	89	84	75	81	49	46	37	48	38	29	40	37	44	39	85	124	56	43	69	76	50	46	54	29

¹ Miscellaneous species: *Anthophora urbana* (1♀N, 1♂), *Bombus pennsylvanicus sonorus* (1♀N), *Ceratina dallatorrena* (1♀N), *Megachile brevis* (1♀N), *Melissodes lupina* (2♀P), *Melissodes roborator* (1♂), *Peponapis pruinosa* (1♀N), *Tripobolus concavus* (1♀N, 1♂). Sleeping (0530): *Agapostemon texanus* (2♂), *Diadasia enavata* (2♂, 2♀N), *Halictus ligatus* (1♂), *Melissodes agilis* (9♂).

TABLE N.—Pollen relationships of the oligoleges primarily associated with the North American species of *Helianthus* (species of bees and sunflowers are arranged phylogenetically)

Bees	Sunflowers																Totals							
	Annui		Ciliares					Divaricati																
	<i>H. petiolaris</i>	<i>H. annuus</i>	<i>H. leucocarpus</i>	<i>H. bolanderi</i>	<i>H. gracilentus</i>	<i>H. pumilus</i>	<i>H. ciliaris</i>	<i>H. mollis</i>	<i>H. occidentalis</i>	<i>H. divaricatus</i>	<i>H. strumosus</i>	<i>H. tuberosus</i>	<i>H. rigidus</i>	<i>H. giganteus</i>	<i>H. grosseserratus</i>	<i>H. nuttallii</i>		<i>H. maximiliani</i>	<i>H. salicifolius</i>	<i>H. microcephalus</i>	<i>H. angustifolius</i>	<i>H. atrorubens</i>	<i>H. radula</i>	
<i>Andrena accepta</i>	x	x	x					x	x	x	x	x	x	x		x	x		x				x	14
<i>aliciae</i>									x	x	x		x						x		x			6
<i>haynesi</i>	x																							1
<i>helianthi</i>	x	x	x						x	x	x	x	x	x	x	x								11
<i>peckhami</i>										x														1
<i>Pseudopanurgus aethiops</i>	x	x	x																					3
<i>rugosus</i>	x	x						x	x		x												x	6
<i>Pterosarus helianthi</i>	x	x																						2
<i>innuptus</i>	x	x									x	x	x			x	x							7
<i>piercei piercei</i>	x	x										x	x				x							5
<i>simulans</i>	x	x															x							3
<i>Perdita albipennis</i>	x	x	x						x				x											5
<i>bequaerti</i>																							x	2
<i>lingualis</i>	x	x	x							x														3
<i>scopata</i>			x																					1
<i>tricincta</i>			x																					1
<i>laticincta</i>	x																							1
<i>tridentata</i>	x												x											2
<i>Dufourea marginata</i>	x	x								x		x	x		x								x	7
<i>Nomia micheneri</i>	x																							1
<i>triangulifera</i>	x	x	x														x							4
<i>heteropoda</i>	x	x	x																				x	4
<i>Hesperapis carinata</i>	x	x	x										x											4
<i>Heteranthidium cordaticeps</i>		x																						1
<i>occidentale</i>			x																					1
<i>zebratum</i>	x	x	x										x										x	6
<i>Megachile parallela</i>	x	x	x						x								x	x					x	10
<i>Exomalopsis pygmaea</i>			x		x					x													x	2
<i>Diadastia enavata</i>			x		x																			3
<i>Swastra helianthelli</i>			x																					2
<i>machaerantherae</i>	x	x																						2
<i>obliqua</i>	x	x	x	x	x				x	x	x	x			x		x						x	15
<i>Melissodes agilis</i>	x	x	x	x					x	x	x	x			x		x	x					x	16
<i>coreopsis</i>	x	x										x												6
<i>gelida</i>	x	x																						2
<i>perlusa</i>	x	x																						2
<i>robustus</i>	x	x	x	x	x																			5
<i>trinodis</i>									x	x	x			x	x								x	10
<i>coloradensis</i>	x	x							x	x		x	x		x								x	8
Totals	28	31	16	3	4	2	3	7	1	11	8	12	12	4	8	3	11	4	2	2	5	8		

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PLATE 1.—*Nomia (Dieunomia) heteropoda* Say, female (above); *Megachile (Argyropile) parallela* Smith, female (below).



PLATE 2.—*Diadasia enavata* (Cresson): female (above); male (below).

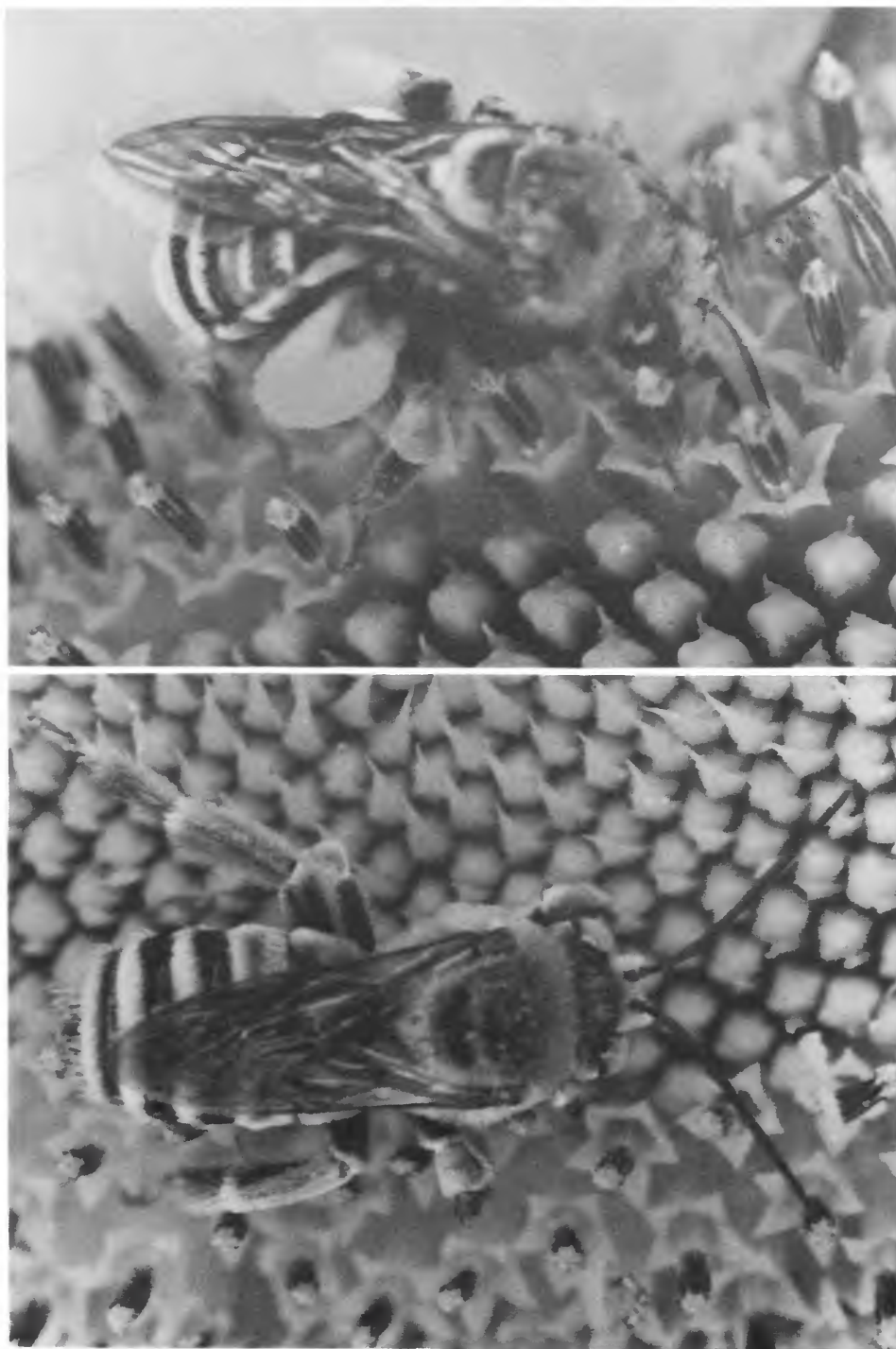


PLATE 3.—*Svastra (Epimelissodes) obliqua* (Say): female (above); male (below).



PLATE 4.—*Melissodes (Eumelissodes) agilis* Cresson: female (above); male (below).



PLATE 5.—*Bombus (Fervidobombus) pennsylvanicus sonorus* Say, worker (above). *Apis mellifera* Linnaeus, worker (below).

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