The Nest Biology of the Bee *Andrena (Ptilandrena) erigeniae* Robertson (Hymenoptera: Andrenidae)

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Detailed biological information on bees of the genus *Andrena* has been scarce (Linsley, MacSwain, & Smith 1952*b*; Michener 1953*a*; Linsley 1958) and for hundreds of species little or nothing is known. Also most of the observations on *Andrena* life histories have been conducted in an opportunistic fashion, largely because of the difficulty in locating nests and the expense and time involved in necessary traveling. Studies have been conducted on the researcher's lawn, in a path on a college campus, near the tent on a camping trip, or incidentally while studying something else. Although several good papers on *Andrena* biology are now extant (Malyshev 1936; Linsley & MacSwain 1959; Michener, Cross, Daly, Rettenmeyer, & Wille 1955; Hirashima 1962; Stephen 1966*a*; Thorp & Stage 1968; Thorp 1969; Rozen 1973) much remains to be done.

The aim of this work is to describe the biology of *Andrena* (*Ptilandrena*) *erigeniae* Robertson. The field work was carried out in Brownfield Woods, northeast of Urbana, Illinois. Laboratory work was done at the Illinois Natural History Survey and the Vivarium of the University of Illinois. The study began about April 1, 1974 and continued through the summer and early fall months of 1974.

At the outset of this study little was known of the biology of *A. erigeniae* or of other members of the subgenus *Ptilandrena*, a small group of solitary bees inhabiting the eastern deciduous forests. This subgenus has yet to be revised and thus an accurate listing of included species is not now possible. However, Mitchell (1960) lists *A. erigeniae* and the following species: *A. distans* Provancher (Robertson's *A. g-maculata*), *A. polemonii* Robertson, *A. krigiana* Robertson and *A. parakrigiana* Mitchell. LaBerge (1967) reduces *A. parakrigiana* to a synonym of *krigiana* and moves this species from *Ptilandrena* to the subgenus *Callandrena*. Therefore, only two species — *distans* and *polemonii* — remain in *Ptilandrena* in addition to *erigeniae*.

Robertson described *A. erigeniae* in 1891 and Mitchell (1960) gave us a more complete description of the species. It is a univoltine vernal bee found frequenting most eastern woodlands. It nests in the woods or along wooded margins where spring beauty, *Claytonia virginica* Linnaeus, is abundant. Robertson (1891) stated that he collected the bee on *Claytonia virginica, Erigenia bulbosa* (Michx.) Nutt. (harbinger-of-spring), and *Hydrophyllum appendiculatum* Michx. (waterleaf). Mitchell (1960) reports only *Claytonia virginica* and *Erigenia bulbosa* as floral records. Three females of *erigeniae* were collected on *Collinsia verna* Nutt. (blue-eyed Mary) by John Marlin at Carlinville, Illinois, May 3, 1971. Other floral records are *Isopyrum biternatum* (Raf.) T. & G. (false rue anemone) on April 15, 16, and 18, 1891 (Robertson, unpublished), and *Dicentra cucullaria* (L.) Bernh. (dutchman's breeches), *Dentaria laciniata* Muhl. (cut-leaved toothwort) both at Carlinville, April 8, 1971 by John Marlin. Knerer & Atwood (1964) reported *erigeniae* from Ontario, Canada, on *Claytonia* and *Prunus* based on less than six specimens, the sexes of which were not noted. LaBerge collected a male of *erigeniae* on *Barbarea vulgaris* R. Br. (yellow rocket) on April 18, 1974, 15 miles southeast of Winchester, Virginia. One specimen collected near Plummers Island, Maryland, April 12, 1917 by J. C. Crawford was taken on *Veronica hederaefolia* L. (ivy-leaved speedwell). Pierce (1918) noted that a stylopized female of *erigeniae* (unverified) was collected at Plummers Island, Maryland, March 29, 1915 by J. C. Crawford on *Erythronium americanum* Ker. (yellow adder's-tongue).

Although *A. erigeniae* has occasionally been collected on a number of plant species, the females appear to be entirely restricted for pollen to *Claytonia virginica* (Fig. 15), which accounts for 91.8 percent of the floral records available for this study (283 specimens with floral data out of 456 examined — see Table 1). The range of *erigeniae* (Fig. 1) is largely coterminous with that of *Claytonia virginica*.

We are grateful to many people for help with various aspects of this project. Special thanks are due to the members of the staff of the Faunistics Section of the Illinois Natural History Survey; to Chris T. Maier, Douglas W. Schemske, and Kathleen A. Schemske, graduate students of the University of Illinois; and to Dr. S. Charles Kendeigh of the University of Illinois, Dr. Robert A. Evers, botanist of the Natural History Survey, and Dr. Charles D.

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COVER PHOTO: *Andrena erigeniae* sucking nectar from flower of *Claytonia*.

TABLE 1.—Floral records for *Andrena erigeniae*.

Plant	Males	Females	Total
Cruciferae:			
Barbarea vulgaris R. Br.	1	0	1
Dentaria laciniata Muhl.	1	0	1
Hydrophyllaceae:			
Hydrophyllum appendiculatum Michx.	2	0	2
Liliaceae:			
Erythronium americanum Ker.[a]	0	1	1
Papaveraceae:			
Dicentra cucullaria (L.) Bernh.	1	0	1
Portulacaceae:			
Claytonia virginica L.	72	188	260
Ranunculaceae:			
Isopyrum biternatum (Raf.) T. & G.	1	3	4
Rosaceae:			
Prunus sp.[b]	?	?	?
Scrophulariaceae:			
Veronica hederaefolia L.	0	1	1
Collinsia verna Nutt.	0	3	3
Umbelliferae:			
Erigenia bulbosa (Michx.) Nutt.	8	1	9
Totals (11 plants in 9 families):	*86*	*197*	*283*
Bees available without floral data:	38	135	173

[a] From Pierce (1918).
[b] From Knerer & Atwood (1964) (undetermined number of specimens).

Michener of the University of Kansas for their kind suggestions and helpful criticism.

We wish to thank the following persons and their institutions for kindly lending specimens under their care: Dr. Howell V. Daly, University of California at Berkeley; Dr. Paul B. Hurd, Jr., U.S. Museum of Natural History; Dr. Michener; Dr. R. M. Miller, Iowa State University; Dr. L. L. Pechuman, Cornell University; Brett C. Ratcliffe, University of Nebraska; and Dr. Jerome G. Rozen, Jr., American Museum of Natural History.

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MATERIALS AND METHODS

Temperature readings were obtained from two centigrade thermometers, one hung from a hook on a tree over the nesting site and the other placed on the ground at the level of nest entrances. Both thermometers were partially shaded.

The bees were timed in their various activities with two stopwatches and a pocket watch. Plaster-of-Paris was poured into the nests and a small trowel and a microspatula used to excavate the nests. Small plastic sandwich bags were used to transport cells and contents to the laboratory. Kahle's solution was used to fix bee larvae and 70 percent alcohol was used to store the larvae after they had been fixed.

Pollen balls were frozen after being measured. Pollen was determined by microscopic examination of material mounted in glycerin jelly on slides made from known pollen sources. Such pollen slides were made from the pollen balls obtained from bee nests or from pollen washed off of the scopae of pinned bees (Thorp 1969).

Measurements were made with Helios dial-calipers and the ocular micrometer of an M5 Wild stereomicroscope. All measurements were either taken in millimeters or converted thereto.

Photographs were taken with a Nikkormat FTN (35 mm) camera with bellows and f3.5 55 mm Auto Micro Nikkor lens. Kodak Panatomic-X and Ektachrome-X film were used. Drawings were made with the use of the M5 Wild microscope and drawing attachment.

Distributional data were obtained from pinned specimens belonging to various major collections, and length of life of adults after emergence was determined from pinned specimens, from personal observations, and the observations of Douglas W. Schemske.

Nests were marked with two large brass paper fasteners, one on each of opposite sides of the entrance. Forty-five of the nests so marked had color coded markers so that the nest could be referred to easily and so that the bee using the nest could be marked correspondingly. Because of the size of the bee, combinations of more than two colors were found to be impractical. The color code was a simple four-way combination of any two of five colors: red, green, blue, yellow, and white. For example, the codes green/white, $\frac{\text{green}}{\text{white}}$, white/green, and $\frac{\text{white}}{\text{green}}$ represent four different nests. Thus by rotating the fasteners 90 degrees with each new nest, four nests could be marked individually while using only two colors. Forty nests were marked in this manner. Other nests located in the area were coded consecutively in a particular color, e.g., red 1, red 2, or blue 17.

Occasionally a glass vial was used as a trap, placed over the nest opening immediately after the bee entered. More frequently the bee was caught by covering the hole with a small screen cone (Linsley, MacSwain, & Smith 1952*a*; Osgood, unpublished). The bees were marked to agree with their respective nests and were released as soon as possible to avoid damage to the insects from excessive handling.

For morphological studies the bee larvae were

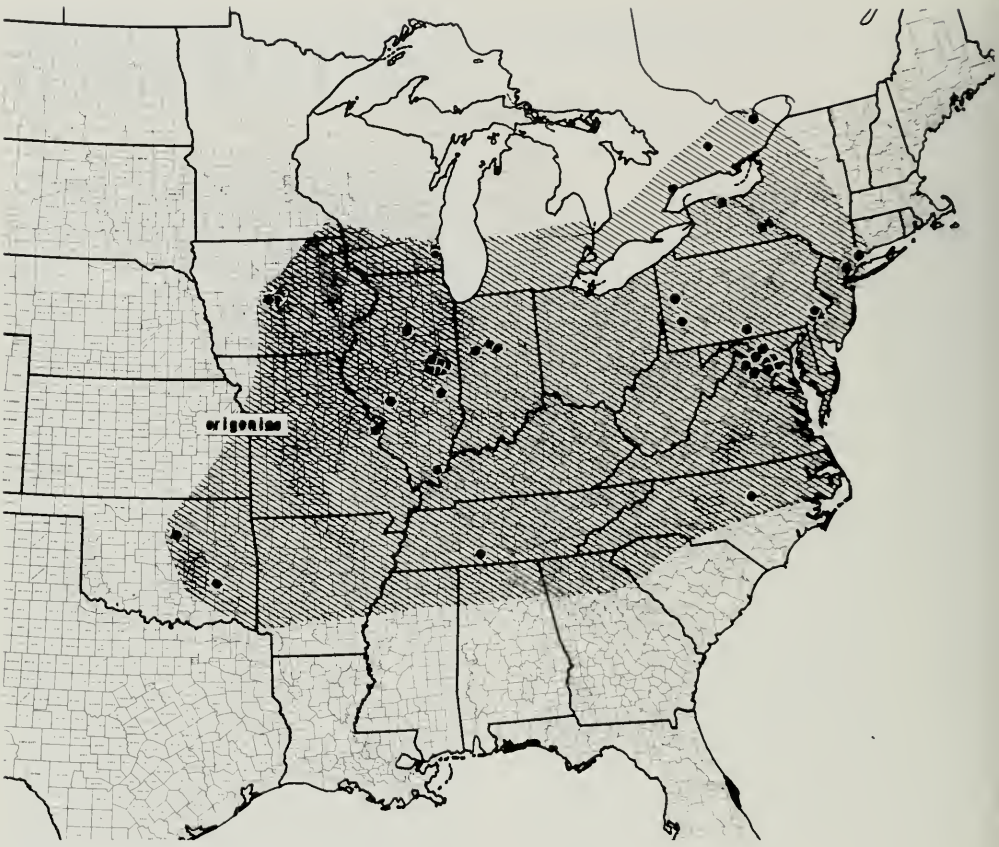

Fig. 1.—Map showing the known distribution of *Andrena* (*Ptilandrena*) *erigeniae* Robertson.

cleared in lactophenol and stained with acid Fuchsin. A compound microscope was necessary to examine details of the spiracles.

DESCRIPTION OF NEST SITE

The nests were located in Brownfield Woods, a rectangular 60-acre remnant of a forested area known as the Big Grove that once occupied a 10-square-mile area in a bend of the Salt Fork River, northeast of Urbana, Champaign County, Illinois (Boggess & Bailey 1964). At the southeast corner of section 34 of T20W, R9E, the woods is located just east of the the now defunct town of Augerville and was at one time known as the Augerville Woods, a frequently recorded locality at the turn of the century. The woods is now owned by the University of Illinois, has been surveyed and soil mapped, and has numbered stakes every 50 m which conveniently locate any section of particular interest.

Bailey (1962) gave the soil characteristics for a small area of the woods. The soil was found to consist of two main types: Birbeck silt loam on 2-4 percent slopes and Sabina silt loam on 0-2 percent slopes. The nest site studied here is located in the later soil type. Information on profiles of this soil type may be obtained from Alexander & Paschke (1972).

The nest site was a low ridge of soil located about 21 m from the forest edge (Fig. 2). The primary area in which nests were located was divided by a depression that frequently retained water after it rained. Thus the site contained two isolated nesting areas about 3 m apart. The larger area ran along the

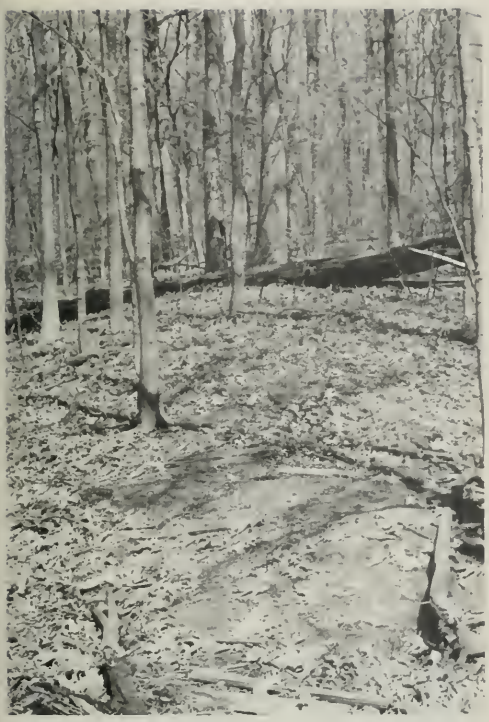

Fig. 2.—View of the larger section of the nesting area looking to the east (April 12, 1974).

Fig. 3.—View of the larger section of the nesting area looking to the east (May 10, 1974). Note the change in the canopy between Fig. 2 and 3.

ridge mentioned above for 12 m and was about 3 m wide (Fig. 2 and 3). The other area was only 3 m long and 2 m wide. The larger area of the nest site was partially covered by fallen leaves, sticks, and patches of moss (Fig. 4). *Claytonia virginica, Dentaria laciniata, Dicentra cucullaria,* and *Viola* sp. grew on both areas. Seedling sugar maple trees (*Acer saccharum* Marsh) also were found on the sites (Fig. 3). The smaller area was without the moss patches of the larger site but was otherwise very similar. A few additional nests were also located along the margin of the woods in a dense patch of *Erythronium* sp.

Osgood (1972) found that the amount of organic matter in the 0_2 horizon was the most important soil characteristic in determining whether or not a particular area may be expected to have solitary bee nests. Areas with high levels of organic matter in the 0_2 horizon had significantly fewer nests. The soil types found in Brownfield Woods average about 2.0 percent in surface organic matter (Alexander & Paschke 1972). This is even lower than the 8.4 percent found by Osgood (1972) for bee nesting areas in the blueberry barrens of Maine.

It was also noted by Osgood (1972) that chosen nesting sites have sparse to moderate plant growth on soils that are well drained with a good surface flow. These characteristics seem to fit the nesting site of *A. erigeniae*. Burrows of *erigeniae* were about 15 cm deep and the water level in the site was sometimes only 8 cm below the deepest cell. Champaign County gets an average of 9 cm of rain for the month of April (Page 1949). With the frequent rainfall during the flight period of *erigeniae*, it is likely that one of the most important factors in the choice of a nest site is the elevation of drainage of the soil. Rau (1935) suggested that the most important factor affecting Missouri populations of *A. erythrogaster* (Ashmead) was the amount of rainfall for the month of April and the resulting level of the subsurface water table.

Fig. 4.—View of nest site showing nest markers and the presence of *Claytonia virginica* and moss. Note the sparseness of leafy vegetation.

PRENESTING BEHAVIOR

Emergence, premating, and mating behavior were not observed. Michener & Rettenmeyer (1956) found that collecting records indicated a proterandry in *A. erythronii* Robertson that did not actually exist. They discovered that *erythronii* usually mated at the nesting site and the females disappeared into the ground soon after mating to begin digging their nests. This left the males as the principal specimens available to collectors. Both sexes of *A. erigeniae* are equally represented in collections taken early in the season. Robertson (1930) found males from April 5 to May 3 and females from March 25 to May 14. Thus, *erigeniae* appears to lack the proterandrous condition reported for some other andrenids. Data from collecting records indicate that mating of *erigeniae* probably takes place on flowers of *Claytonia virginica*.

LOCATION OF NESTS

The nests of *A. erigeniae* were first found under leaves and this was accomplished by following a pollen-carrying bee. When the leaf was overturned, a nest entrance was often exposed. This method can be used to locate many other vernal *Andrena* nests in wooded areas (Stephen, Bohart, & Torchio 1969; LaBerge, unpublished data). Although many nests are found beneath leaves, leaf litter is not necessarily an indication of nest sites. In many areas of Brownfield Woods that had leaf litter closely resembling that at the nest sites no nests were found. In general, no nests were found where the leaf litter was thick enough to keep the ground beneath constantly wet.

Nesting beneath a thin layer of fallen leaves probably serves primarily to protect the nest from heavy spring rains that commonly fill in the burrows of unprotected nests. The leaves may also protect the nest somewhat from predators and parasites, functioning in some way in nest recognition by the bees. Recognition of its nest by the bee probably depends on a combination of both olfactory and visual cues. Dependence upon some sort of cue is shown by the observation on April 10, 1974 that a female twice tried unsuccessfully to locate her nest from which the covering and surrounding leaves had been removed. Only after the third attempt did the bee succeed in finding the entrance.

With respect to nesting, *A. erigeniae* appears to be gregarious (Fig. 4). *A. carlini* Cockerell, found nesting in the same area, seems, on the other hand, to be rather solitary. The density of nests of *erigeniae* ranged from 1 to 21 per m^2, whereas that of *carlini* ranged from one to three nests per meter. This may indicate only that *carlini* prefers another soil or cover type for nesting aggregations. Atwood (1933) records dozens of nests of *carlini*, "close together," in northeastern Canada.

Possible reasons for gregarious nesting in solitary bees have been proposed (Perkins 1919; Michener & Rettenmeyer 1956; Stephen 1966*a*). No new light has been shed on this question during the course of this investigation. However, it would be interesting to capture and mark all emerging bees from a particular nest site and determine exactly what percentage of the population disperses and whether the dispersing segment is from a group of relatively late emergers as compared to the normal range of emergence times. There would seem to be obvious selective advantage for nesting in the same area where the parent had nested. Perhaps the earliest bees to emerge nest in the most suitable sites of the immediate area. The activity of these bees or the presence of old nests in the site may cause the area to be attractive (by means of olfactory stimuli) to later emerging bees until, at a certain density, the area becomes saturated with nests, at which time subsequently emerging bees would be forced to disperse. Such dispersal, triggered by whatever mechanism, seems to be almost a necessity for the survival of the species because of the possible deleterious effects of a build-up in populations of inquilines, parasites,

and predators (or disease) in a concentrated nesting aggregation.

NEST CONSTRUCTION

Digging by female bees apparently begins soon after emergence. Nests of *A. erigeniae* were found first on April 3, 1974, although adult bees were observed above ground and collected on March 31, 1974 by Douglas W. Schemske. Digging may begin horizontally on the side of a small raised lump of soil, or, more typically, vertically under a leaf or stick, on bare soil, on or through moss (Fig. 5), or in a depression already present at the site. One female observed searching for an appropriate nest site on April 13, 1974 at about noon behaved similarly to *A. erythronii* described by Michener & Rettenmeyer (1956). This bee dug a partial hole in one area and then abandoned it to dig a few centimeters away. Once the final site was chosen, the bee continued to dig as long as it was observed.

While digging a nest, the female enters the hole head first and scrapes off small, irregularly shaped and sized particles of dirt with her mandibles and prothoracic legs. As the digging progresses the bee works in a circle around the perimeter of the nest in either a clockwise or counterclockwise direction.

Fig. 5.—Typical nest entrance (center of photograph) of *Andrena erigeniae*. Note that the tumulus has been washed away by rain.

As small particles of dirt are scraped away, they are collected by the legs and passed back to the metathoracic legs whereby they are pushed out of the burrow as the bee backs out. The abdomen is also used to flick out these small pellets of dirt and to push them away from the nest opening. Apparently the details of the digging process are quite similar for many species of *Andrena*. Sivik (1954) describes essentially the same process for *A. macra* Mitchell. Michener & Rettenmeyer (1956) offer similar details for *A. erythronii*.

As a result of bringing this soil to the surface, a small, usually circular or oval pile of particles called a tumulus collects around the nest entrance. The tumuli vary in size from 1.5 to 6 cm in diameter and from 0.25 to 1.5 cm in height (12 measurements).

At times during nest construction, the dirt particles may partially obscure the nest entrance. This condition is temporary and may last only for the period of time it takes the bee to bring up another load of soil particles. The tumulus may sometimes be helpful in locating new nests, as its edges are occasionally visible beneath leaves. The short-lived tumuli are usually completely obliterated by the first rain after construction, leaving only the entrance hole to mark the presence of the nest (Fig. 5 and 6).

A. erigeniae, unlike *A. erythronii* (Michener & Rettenmeyer 1956), leaves its burrow open during the foraging period of the day. However, after making the last pollen-collecting trip of the day, the bee normally remained in the nest after unloading her pollen, and after a few minutes could be observed bringing up soil particles to form a small plug about a centimeter below the surface. Thus, the nest was plugged with the bee inside. The soil from such plugs

Fig 6.—Female *Andrena erigeniae* in typical pose at the nest entrance.

may have come from the walls of the main shaft of the burrow, or, more likely, may have come from a new cell being constructed in the burrow. Linsley & MacSwain (1959) noted that *A. complexa* and *A. suavis* (both belonging to the *Geandrena* LaBerge, 1964) formed similar nest plugs at the end of daily foraging activity. This behavior has also been observed for the *Diandrena* by Thorp (1969). *A. complexa* was found to make about four collecting trips to complete a 50-mm pollen ball (Linsley & MacSwain 1959). Occasionally *erigeniae* made five trips a day but more frequently made only four or less, the latter especially if weather conditions became limiting. Thus, if these four or five trips are all that are required to complete a pollen ball, the plug is apt to be formed from soil removed during the construction of a new cell. The following day the plug was removed before the onset of foraging activity.

Nests of *A. erigeniae* were found to be 15 cm or less in depth (Fig. 7). The main shaft of the burrow was vertical or nearly so, and essentially straight except for necessary alterations in heading to avoid obstacles such as roots and small stones. At a depth of from 8 to 15 cm the burrow usually made a sharp change in direction and proceeded horizontally or downwards for from 3 to 6 cm. In general outline (Fig. 8–11), the nests were quite similar to that drawn by Thorp (1969) for the *Diandrena*.

Two observations were made of *A. erigeniae* filling in nests prior to abandonment (Fig. 12). The bee enlarged the opening around the entrance to approximately twice its diameter by breaking off small particles of soil with its mandibles. The soil was packed into the nest lumen until the opening was entirely obstructed. The bee then walked away to rest on a leaf and, after a few minutes, flew away.

The main shaft of the burrow of *A. erigeniae* is simple and unbranched. The number of cells found in a nest varies from 3 to 14, but is commonly 6 to 8. Laterals leading to cells are dug along the main shaft of the burrow on all sides and extend from 2 to 5 cm from the main shaft. Cells were found from 6.5 to 15 cm below the surface. This would put them below the frost level except on very cold years. Lateral connectives leading from the main shaft of the burrow to the cells are open only during actual provisioning. There was no evidence that the bees closed the laterals between pollen-

Fig. 7.—Excavated nest (plaster-poured) of *Andrena erigeniae* showing the position of one cell at the lower left.

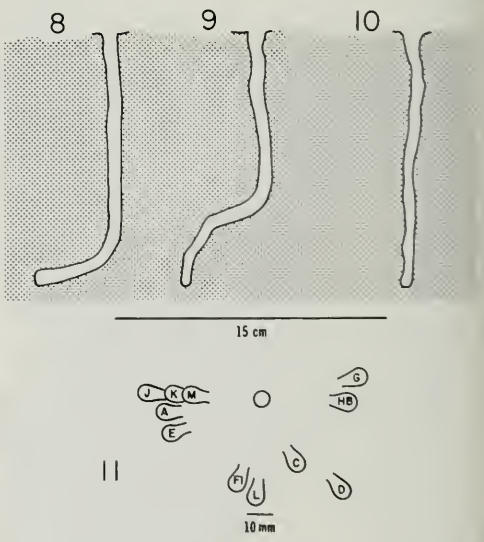

Fig. 8–11.—Nest architecture of *Andrena erigeniae* nests. 8–10.—Lateral views of three nests, the first typical, the next two variations. 11.—Diagram of the relative positions of the cells in a single nest as seen from dorsal view. Letters indicate relative depth of each cell with A indicating the shallowest and oldest cell. Two letters indicate two cells, one above the other.

Fig. 12.—Female *Andrena erigeniae* filling in nest prior to abandonment (May 10, 1974).

collecting trips as do *A. accepta* (Rozen 1973). Upon completion of the pollen ball and subsequent oviposition, the laterals are packed full of loose dirt. It was not possible to trace the path of a lateral to the main shaft. This made the identity of certain cells doubtful when the exposed nest was near other nests. In general, the direction in which the cell plug pointed was used to determine the relationship of particular cells to a particular burrow.

In nests dug before the bee had completed provisioning, the incomplete cell was the deepest and was located at the end of the burrow. No nests were found to have more than one incomplete cell. In nests dug later in the season, the cells deepest in the ground contained pollen balls that had been only partially consumed. Cells closer to the surface in these same nests contained larvae that had completely eaten their provisions. Therefore, unlike *A. viburnella* (Stephen 1966*a*), *A. erigeniae* is a progressive nest builder and constructs horizontal rather than vertical cells.

From our observations, nesting took place from the last week of March until about the second week of May. Robertson (1929) lists the flight period as 50 days, or from 10 days after the start of blooming of *Claytonia virginica* to 10 days before the end of the blooming period.

Variability in the time when nesting activity began is thought to be mainly the result of a normal range in emergence of females, but possibly some late nests are actually the second nests of some bees. Marking procedures did not help solve this problem, as the paint was worn off of most bees too soon. However, while marked, none were observed going to more than one nest.

Nest diameters varied within individual nests. Average nest diameters ranged from 4.75 ± 0.06 mm (N=12) to 6.87 ± 0.36 mm (N=11) for 10 nests measured. An overall average burrow diameter was 5.70 ± 0.09 mm (N=134) for 13 nests measured.

The construction of cells was similar to that described by Michener & Rettenmeyer (1956) for *A. erythronii*. Cells were apparently constructed in a small cavity created by the bee and lined with a layer of packed soil about 0.5 mm thick. This lining was covered with a very thin layer of material that probably was related to silk in composition. This lining waterproofs the cell (Thorp 1969; Rozen 1968). The surface of the lining appeared very shiny and was covered by scattered droplets of liquid (Fig. 13). It was not determined whether these droplets were water or nectar or were of some other composition. An attempt to run a simple test on the contents of some of these droplets failed because of their very small size and the necessity to relocate them to a glass plate for the test. It is reported in the literature (although untested) that these droplets are nectar (Malyshev 1936; Michener & Rettenmeyer 1956). Linsley & MacSwain (1959) observed similar droplets in the cells of *A. complexa* and *A. suavis*.

Fig. 13.—Cell, pollen ball, and egg of *Andrena erigeniae*. Note the small droplets of liquid on the cell wall, and that the egg touches the pollen ball on one end only.

BEHAVIOR OF BEES AT THE NESTING SITE

Adult females of *A. erigeniae* take 33.29±2.28 minutes (N=63) to make a pollen-collecting trip. Bees often waited near the entrance of the nest after unloading their pollen. Because of this, the time spent in the burrow can be divided into two measurable categories. One is the time from entering the burrow until the bee returns to the top (time required to unload the pollen) and the second is the total time spent in the nest before the next trip. The average time spent unloading pollen was 5.16±0.12 minutes (N=96), while the average time in the nest between trips was 7.54±0.56 minutes (N=65).

While in the nest the bee often stayed just below the surface or with only the head and thorax exposed (Fig. 6) and sudden movements by the observer at such times caused the bee to retreat by backing down the burrow. Most bees produced a faint buzzing sound when disturbed in this manner. After a few minutes the bee would reappear at the surface. Aside from bees digging nests or retreating from the observer, no bees were ever seen backing into or out of nests. One bee which had a vertical nest opening was observed to come to the surface on the side of the burrow that became the top of the vertical entryway. Thus when it reached the entrance it was upside down. It crawled around the entrance until it was right side up before flying.

Some bees flew off directly from the nest entrance. Others, especially on cooler days, crawled out of the nest slowly and sat on a nearby leaf or some other object before leaving. Bees bringing in loads of pollen showed a similar range of behavior. Linsley, MacSwain & Smith (1955) found that *A. mojavensis* Linsley & MacSwain, *A. deserticola* Timberlake, and *A. oenotherae* Timberlake usually landed directly at the nest entrance. On the other hand, Michener & Rettenmeyer (1956) noted that *A. erythronii* only rarely flew directly to the nest. Behavior of *A. erigeniae* was variable in this regard. Some bees landed practically on the rim of the nest, paused a moment, then entered. Others, again especially on cold days, landed sometimes as much as a meter from the nest and either walked to it or rested on a leaf for a while and then made a series of short flights to the nest. Bees almost always paused momentarily before entering or leaving the nest. During this pause it was very easy to frighten the bee. If the bee was about to enter the nest, it would fly away and return after a minute or so. One bee was frightened off four times in succession, three times by movements of the observer and once by a Syrphid fly hovering over the nest site.

An occasional bee left the nest and returned with no pollen. This was more common before April 15. One such bee left its burrow and was gone for 72 minutes before returning without any pollen. When a bee returned without pollen it paused momentarily at the entrance, entered, and returned to the surface in less than a minute (usually 40–50 seconds).

On cold days or days when the sky was dark and overcast the bees remained at the entrance of their burrows for long periods. Heavy rain prevented flight but both *A. carlini* and *A. erigeniae* were observed in flight during a light shower of rain.

Like *A. erythronii* (Michener & Rettenmeyer 1956), *A. erigeniae* did not exhibit aggressive behavior toward other bees. The observer placed a Nabid bug into the nest of one bee while the bee was present to see if any active defense of the nest could be observed. There was no indication of a struggle but the bee remained out of sight in the nest for the rest of the afternoon. The females of *erigeniae* are unable to sting so it would appear that their best strategy would be avoidance tactics rather than aggressive defense of the nest.

Although the nests of other species of bees were not abundant, at least two other species of *Andrena* (*carlini* Cockerell and *nasonii* Robertson) and one species of *Lasioglossum* were observed nesting in the *erigeniae* nesting sites.

PROVISIONING

Pollen collected by *A. erigeniae* is entirely that of *Claytonia virginica*. The pollen balls were spherical, pink, and moist. The color often changed to pale yellow after being exposed to air or after being partially consumed by either the larval bee or an inquiline. The pollen balls ranged in size from 3.2 by 3.35 mm to 4.3 by 4.6 mm in the two opposite diameters. The average size was 3.81±0.83 mm by 3.99±0.091 mm (N=24). This is smaller than measurements reported for *A. erythronii*, a larger bee, by Michener & Rettenmeyer (1956). Linsley & MacSwain (1959) gave the weight of the pollen ball of *A. complexa* as 0.05 g. Pollen balls of *erigeniae* ranged from 0.017 to 0.057 g with an average of 0.037±0.0022 g (N=26). The incomplete pollen ball in Fig. 14 weighed 0.0095 g. A remarkable variation existed in the size of pollen balls from a single nest. For example, one nest contained six pollen balls that weighed: 0.057, 0.028, 0.021, 0.025, 0.035, and 0.042 g.

Temperature and the opening of *Claytonia* flowers apparently set the early limits to daily foraging behavior of *A. erigeniae*. No bees were observed bringing in pollen loads before 10:00 a.m. (N=204). The end of daily foraging was probably determined by the completion of a cell (Linsley & MacSwain 1959), but may have been caused by dropping temperatures, lowering of light intensity, or rain. It is suggested that the completion of the pollen ball may be the primary reason for the end of pollen-

Fig. 14.—Incomplete pollen ball of *Andrena erigeniae*. Note the rough surface of the pollen ball.

collecting for the day. This is because most bees seemed to finish foraging between noon and about 2:30 p.m. (N=29) when it was still light and often quite warm. Pollen availability may also play a part in this. By midafternoon most of the available *Claytonia* pollen would probably be gone, so that at a certain point a bee would find the energy expended to collect a load of pollen the limiting factor. Data on the length of pollen-collecting trips indicated that the first and last trips of the day were often the longest for an individual bee.

Time expended per trip in collecting pollen varied from 10 to 92 minutes. Michener & Rettenmeyer (1956) found that trips for *A. erythronii* varied from 27 to 235 minutes. Stephen (1966*a*) reported the mean trip length for *A. viburnella* as 26 minutes (from a range of 18–52 minutes) and suggested that the difference between the times for *erythronii* and *viburnella* was because *erythronii* was oligolectic and *viburnella* was polylectic in foraging habits. Although the mean time spent collecting pollen was longer for *A. erigeniae* (about 33 minutes) than for *viburnella*, Stephen's explanation may not be correct. Generalizations about the foraging times with respect to floral constancy are entirely unreliable when generalizations are based solely on the behavior of locally studied populations. This is a consequence of the range of variability within a species of bee and between various populations of that species along with an obvious variability in the availability of proper nesting site locations. In fact, *erythronii* (Michener & Rettenmeyer 1956) foraged much earlier in the season than either *erigeniae* or *viburnella* (Stephen 1966*a*). Thus colder weather may have forced the bees to make more frequent rest stops between flower visits. Such activity has been observed for *erigeniae* on cold days. Contrary to the assumption of Stephen (1966*a*) an oliogolectic bee may at times find suitable nest sites directly among the host plants and require only very short trips to complete a pollen load.

Time spent in the nest between trips by *A. erigeniae* averaged about 7.5 minutes from a range of 4–31 minutes. Michener & Rettenmeyer (1956) observed a range of 17–88 minutes for *A. erythronii*. Stephen (1966*a*) observed a range of 6.5–33 minutes for *A. viburnella*. He attributed the difference between *viburnella* and *erythronii* to the fact that *erythronii* fashions a pollen ball while *viburnella* does not. *A. erigeniae* rolls its provisions into a ball very much like that of *erythronii;* therefore, it is unlikely that the time differences noted above are due to the particular difference in behavior noted by Stephen. The difference may more likely arise from the lower temperatures that characterize the earlier foraging of *erythronii*, if any difference other than the bees being of different species is to be accounted for.

As previously mentioned, pollen collected by *A. erigeniae* was fashioned into a largely spherical ball. Michener & Rettenmeyer (1956) noted that *A. erythronii* worked its pollen into a ball as it was brought into the nest. Incomplete, smaller balls were found to be drier and less smooth than completed balls. Linsley & MacSwain (1959) have noted the same sort of behavior for *A. complexa* and *A. suavis*. The pollen balls were formed by *erigeniae* in a similar manner (Fig. 13 and 14).

Very little quantitative observational data were obtained of bees actually gathering pollen. However, many *A. erigeniae* were seen visiting *Claytonia virginica* for both pollen and nectar. In gathering pollen, the bee encircled the stamens with its legs and bunched them together in the center of the flower (Fig. 15). The bee usually moved around the flower in a circle during this procedure. Pollen was thereby rubbed from the anthers onto the bee's body and legs and moved back to the scopae. Visits to flowers usually lasted only a few seconds. Two bees collecting pollen from *Claytonia virginica* on May 7, 1974, were observed to remain on the flower for 10.5 and 12.5

Fig. 15.—Female of *Andrena erigeniae* collecting pollen from *Claytonia virginica*.

seconds. Another bee stayed on a flower for 10.7 seconds drinking nectar.

As discussed above, on cool days a bee often spent a lot of time resting on leaves. A bee observed on May 7, 1974 drank nectar from one flower, crawled off to a nearby leaf, then visited three flowers, and flew to another leaf. Another bee was observed resting on a leaf for 49 seconds, spent 5 seconds on a flower, fell off, rested 64 seconds, visited another flower, and crawled back onto the first flower.

As the flight period of *A. erigeniae* progressed during May, the tree canopy gradually closed. *Claytonia virginica* was noted by Schemske (personal communication) to set seed rapidly as the light intensity under the canopy decreased. By the last of April only isolated patches of *Claytonia virginica* were still available to the bees for pollen. By the middle of May the plant was no longer in flower in the woods.

DEVELOPMENTAL OBSERVATIONS

A. erigeniae in our study area probably began nesting activities in 1974 about, or shortly before, March 31. Nests dug previous to and on May 10 contained only eggs. Nests dug on May 11 and 15 contained first instar bee larvae about the same size as the eggs (Fig. 16). On May 28 a nest was dug that contained some large bee larvae that had consumed about one-half to three-quarters of their pollen balls. Other larvae in this same nest had completely eaten their pollen except for a few grains stuck to their ventral surfaces. Nests dug on July 3 contained only postdefecating larvae.

Feeding of the larva produced a small pit in the pollen ball immediately beneath the head of the larva. The pollen was gradually encircled as the larva grew, until finally only a small amount remained on the ventral surface of the larva. Larvae defecated on the distal surface of the cell wall. The feces formed a yellowish mass that contained the empty shells of pollen grains.

All species of *Andrena* thus far studied overwinter as adults in the cells of their nests (Michener & Rettenmeyer 1956). *Andrena* do not spin a cocoon when they pupate (Stephen, Bohart & Torchio 1969). Pupation takes place in late summer and adulthood is reached sometime in the fall (Thorp & Stage 1968). *A. erigeniae* were found to be in pupal stage on August 12 and some of the pupae had fully formed

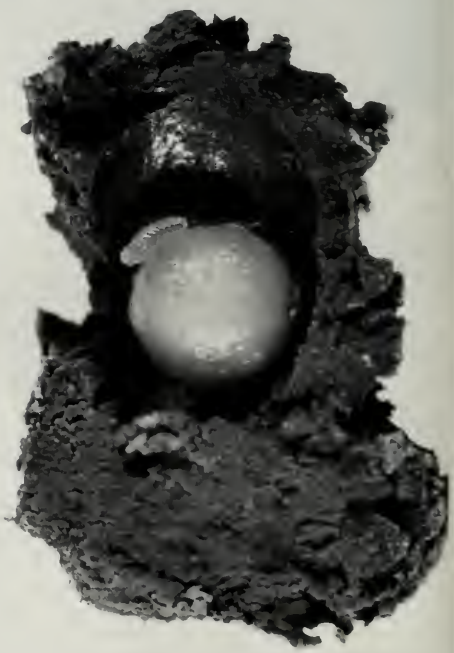

Fig. 16.—Newly hatched larva of *Andrena erigeniae* resting on its pollen ball.

and almost fully colored adult integument beneath the pupal integument. It is evident from this that *erigeniae*, like other *Andrena*, does not spin a cocoon and overwinters in the cell as an adult.

DESCRIPTION OF EGG

The egg of *A. erigeniae* was located on the top of the pollen ball with only the distal end (relative to the cell plug) touching the pollen (Fig. 13). This is slightly different from the observations made for other species of *Andrena*. The eggs of *A. erythronii* (Michener & Rettenmeyer 1956), *A. suavis* and *A. complexa* (Linsley & MacSwain 1959), and *A. accepta* (Rozen 1973) touch the pollen ball at both ends. It was observed that the egg readily stuck to the pollen ball if contact was made between the two. Almost all *erigeniae* eggs were attached at both ends after being transported to the laboratory at which time some eggs were found lying flat against the pollen ball, as figured for *erythronii* (Michener & Rettenmeyer 1956).

The chorion of the egg was very thin and delicate. As a result, many eggs were broken before they could be measured. Eggs of *A. erigeniae* were white and slightly bowed, much like those described for *A. placida* by Thorp & Stage (1968). The egg measured 2.15±0.073 mm (N=13) in length and 0.51±0.015 mm (N=13) in diameter. This is roughly similar to the dimensions reported for several other *Andrena* (Michener & Rettenmeyer 1956; Hirashima 1962; Rozen 1973). *A. rhodotricha* Linsley has an egg 3 mm in length and less than 1 mm wide (MacSwain 1945). Thorp & Stage (1968) reported the egg of *placida* as 2.4–2.7 mm by 0.57–0.75 mm.

DESCRIPTION OF POSTDEFECATING LARVA

The postdefecating larvae of *A. erigeniae* like other *Andrena* (Michener 1953*b*; Michener & Rettenmeyer 1956; Stephen 1966*b*; Thorp & Stage 1968; Thorp 1969; Rozen 1973) are C-shaped with distinct transverse dorsolateral tubercles. Thoracic tubercles are rectangular in lateral view while abdominal tubercles are more rounded (Fig. 17). Rozen (1973) described the postdefecating larva of *A. accepta*, a member of the subgenus *Callandrena*. The larva of *erigeniae* more closely resembles the larva of *accepta* than any other species yet described.

Head (Fig. 18, 19, and 20): as in *A. accepta* (Rozen 1973) except parietal bands not apparent. Mandible (Fig. 21): upper apical margin with three large teeth, lower margin without small denticles.

Body (Fig. 17, 22, and 23): as in *A. accepta* (Rozen 1973) except without setae, dorsum nonspiculate; 10th abdominal venter nonspiculate; anterior surface of ventral tergites densely spiculate; posterior surface of ventral tergites sparsely spiculate; spicules extending laterally to just above the spiracles.

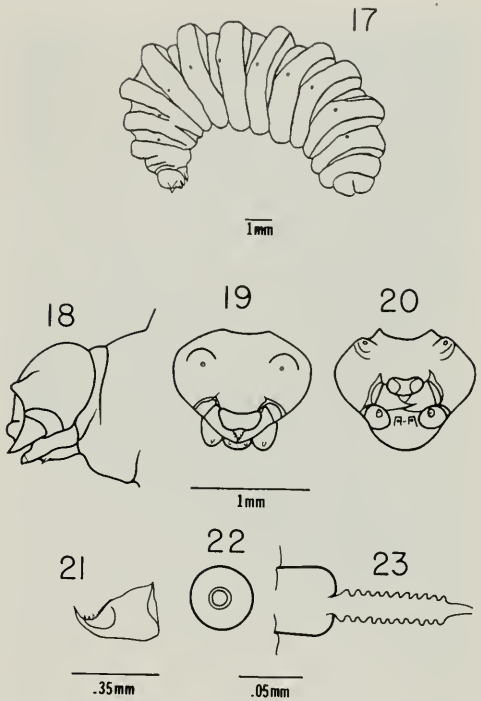

Fig. 17–23.—Drawings of postdefecating larva of *Andrena erigeniae*. 17.—Lateral view of larva. 18.—Lateral view of head capsule. 19.—Frontal view of head capsule. 20.—Ventral view of head capsule. 21.—Ventral view of right mandible. 22.—Surface view of spiracle. 23.—Longitudinal section of spiracle.

INQUILINISM AND PARASITISM

Female bees carrying pollen were observed being shadowed or followed closely by the anthomyiid fly, *Leucophora obtusa* (Zetterstedt). This fly was frequently seen resting on plants or on the ground in the nesting sites. Bees weaving over the area searching for their burrows were often followed at a short distance. A fly would almost exactly follow the rapid meandering flight of the bee. When the bee entered its nest, the fly landed, entered, and then left a few minutes before the bee emerged. Occasionally the bee would land clumsily a short distance from the nest and then turn and face the fly which had landed close behind. A face-off a few centimeters in diameter then took place with the two insects walking in a circle while facing each other. The bee occasionally attacked the fly during such an encounter.

Similar observations have been made by others. Hirashima (1962) observed "a small dipterous fly

belonging to the family Muscidae" pursue the female of *Panurginus crawfordi*. Hirashima found the larvae of these flies consuming the pollen in bee cells. Unfortunately these flies were not determined as to species. Michener & Rettenmeyer (1956) observed *A. bipunctata* females being followed by *Leucophora obtusa*. Huie (1916) observed the behavior of a Scottish anthomyiid that chased the females of *A. analis* Panzer.

How the fly larvae get into the bee cells is unknown. According to Stephen, Bohart, & Torchio (1969) anthomyiid flies of the genus *Hammomya* (=*Leucophora*, Huckett 1940) lay their eggs on the host's pollen mass as it is being carried into the nest. However, Michener & Rettenmeyer (1956) noted a different type of behavior for the *L. obtusa* after they observed it following *A. bipunctata*, which leaves its burrow full of loose particles of dirt. After the *bipunctata* female had entered its nest, the fly was observed to land and insert several elongate white eggs into the loose soil of the tumulus (Michener & Rettenmeyer 1956). It is interesting that the larvae of this fly were not found in any of the nests of *bipunctata* which were later excavated (Michener 1974, personal communication). Huie (1916) and Charbonnier (1901) have observed an anthomyiid fly that entered the bee's nest after the bee had left, came out of the hole, and then re-entered backwards to oviposit. This behavior was not observed with *L. obtusa*.

If the anthomyiid eggs are laid on the pollen being carried by the female bee, why are they not destroyed either accidentally or directly by the bee while it is removing the pollen load or shaping it into a ball? Certainly the eggs are much larger than the individual pollen grains. It is difficult to believe that the bee would not recognize such large objects as foreign and either destroy or remove them from the nest. This would seem to be especially true for those fly eggs that happened to be transmitted to the cell on the first load of pollen for that cell.

Excavation of the nests of *A. erigeniae* commonly revealed the presence of various-sized fly larvae in the cells. One cell was found to contain three diptera larvae, of which two were large fourth instar larvae while the third was very small and thought to be a first instar larva. Several other cells contained two large larvae and others contained only one or the larva of *erigeniae* (Fig. 13 and 14). The rate of inquilinism varied. Some nests were almost entirely devoid of bee larvae because of the presence of these flies. Others were not affected. The infestation seemed to be heaviest where the nest density was the highest. The three nests dug on April 25, 1974 at a low density nesting area were free of inquilines.

Some discussion seems justified concerning the observation that three fly larvae of two different sizes were found in one cell. How are larvae of different sizes in the same cell? The first possible answer is that the eggs of the fly were brought into the nest by the bee at two different times. If, for example, the bee brought in the first two fly eggs with a load of pollen and was unable to fly for the next couple of days due to inclement weather, the first two eggs would get a head start on any eggs that happened to be brought in with the next pollen trips. Perhaps a better answer is that the food supply in the cell is only enough to support two fly larvae to adulthood. If this is so, then the third larva might merely have been out-competed for the available food and was stunted from lack of sufficient nourishment. A third possibility is that the fly eggs are deposited in the burrow and, after hatching, the larvae actively seek the cells. If this is the case, the size difference might be accounted for simply by different arrival times of the larvae. Michener & Rettenmeyer's (1956) observation that the fly inserted eggs into the tumulus lends support to this idea.

Note that these flies are referred to as inquilines and not parasites. This is because they do not depend on the body of the bee larva as their source of nourishment (Huie 1916; Askew 1971) and because they may not be directly responsible for the demise of the bee (Hirashima 1962). One excavated cell contained both a first instar bee larva on the pollen ball and a first instar dipterous larva on the wall of the cell (Fig. 24). Some nests contained cells with diptera larvae and a mold on the pollen ball (Fig. 25). Other cells contained diptera larvae and the remains of the pollen ball, which had been reduced to a pale yellow, soupy mass. Hirashima (1962) has suggested that the change in the consistency of the pollen mass may cause the demise of the bee larva. Huie (1916) reported an anthomyiid fly larva that devoured a bee larva that had stopped feeding after its pollen became moldy. The fly larva consumed the fungus-ridden pollen ball first and only attacked the bee larva after all other food was gone.

Although no quantitative records of developmental times were obtained for the Anthomyiid flies, they appeared to undergo a very rapid development as compared to that of the bee larvae feeding on the same materials. After reaching the fourth instar, the diptera larvae burrow out of the cell and pupate in the surrounding soil. Collecting records (Huckett 1940) indicate that this species is univoltine and overwinters in the soil. Pupae of our flies are being kept to compare with adult *L. obtusa* observed around the nesting site.

L. obtusa is not restricted to *A. erigeniae* pollen balls. It was also observed following a small *Simandrena* (probably *nasonii* Robertson) that was nesting in the *erigeniae* nesting site. Michener & Rettenmeyer (1956) found it following *A. bipunctata* in Kansas. Collecting records indicate that it is found as far west as California (Collin 1920; Huckett 1940)

Fig. 24.—Larva of *Andrena erigeniae* on a pollen ball and a small dipterous larva on the wall of the cell.

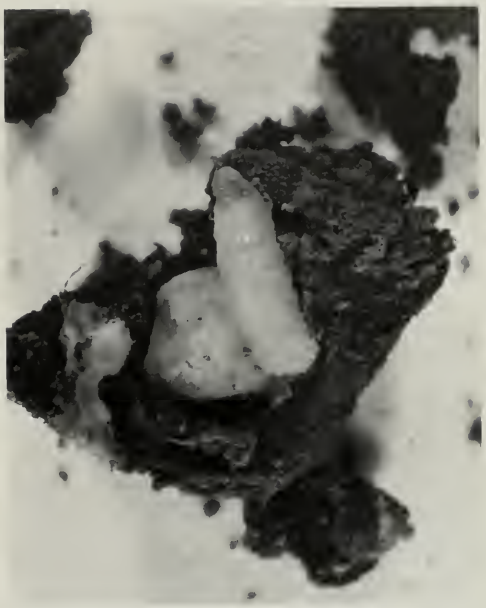

Fig. 25.—Large dipterous larva found in the cell of an *Andrena erigeniae*. Note that no bee larva was present, and the large amount of deteriorating pollen and fungus in the cell.

and its presence has been noted in Great Britain. Therefore, it undoubtedly subsists on the provisions of a number of different species of bees.

During the course of this study two species of *Nomada* (Anthophoridae) were captured flying over the nest site and visiting flowers in the nesting area. However, none were seen entering the nests of *A. erigeniae*.

A. erigeniae is sometimes parasitized by stylopids (Robertson 1891; Robertson 1910; Robertson 1918; Pierce 1909; Pierce 1918; Salt 1927). Of the pinned museum specimens examined during the course of this study only 2 out of 430 were stylopized. The data on these two specimens are: Mahomet, Illinois, April 26, 1925, coll. A.S.B. (Beardsley); Stillwater, Oklahoma, III-24-1936, coll. Myron Maxwell. Both specimens may be designated as female and neither was carrying pollen when collected. Salt (1927) noted that he had examined two females of *erigeniae* that were stylopized. Pierce (1918) described *Stylops erigeniae* from two specimens taken from a female *erigeniae* (unverified identification). This bee was collected at Plummers Island, Maryland, March 29, 1915, by J. C. Crawford. Pierce (1918) also noted a stylopized *A. erigeniae* collected at Carlinville, Illinois, April 1, by Charles Robertson.

A few other insects that might be considered to be accidental intruders were occasionally seen entering the nests of *A. erigeniae*. These include the nitidulid beetle, *Glischrochilus quadrisignatus* Say; the hydrophilid beetle, *Sphaeridium scarabaeoides* L. (both identified by Lloyd Davis), and an undetermined ant (Formicidae). None of these insects remained in the burrows for long and seemed to have entered the burrow by chance. Other accidentals found associated with the cells of *erigeniae* were enchytrid earthworms of undetermined species (identified by L. J. Stannard). These worms were found in two cells from different nests. One of the cells had been penetrated lengthwise by a small root. No bee larvae were found in either cell, although the remains of the pollen ball were still evident.

The role of fungus in destroying bee larvae and provisions is not well understood (Linsley 1958; Stephen, Bohart, & Torchio 1969). Although fungus apparently does destroy cells, it appeared that many of the cells that had fungus had previously been occupied by inquilines (Fig. 25) or disrupted by roots. It would seem likely that a moist environment like the soil in the nest site would make the nests very susceptible to fungus. Do the bees produce some type of fungal inhibitor (suggested by Stephen, Bohart, & Torchio 1969) that is incorporated into the cell or provisions during construction? Perhaps such a substance is manufactured by the bee larva. Further work in this area is needed.

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