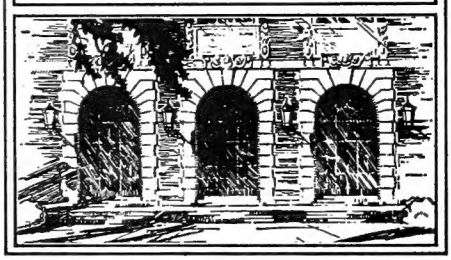

THE NEST BIOLOGY OF THE BEES

Andrena (Melandrena) regularis Malloch and *Andrena (Melandrena) carlini* Cockerell (Hymenoptera: Andrenidae)

Martha Northam Schrader Wallace E. LaBerge

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Cover Illustration.—*Andrena carlini* resting on flowers of *Dentaria laciniata* in Brownfield Woods, Urbana, Illinois (Photograph by Joseph Laury Luth)

The Nest Biology of the Bees *Andrena (Melandrena) regularis* Malloch and *Andrena (Melandrena) carlini* Cockerell (Hymenoptera: Andrenidae)

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Detailed biological information on bees of the genus *Andrena* is scant and for most species nothing is known. Several valuable papers concerning *Andrena* biology are available (Davis & LaBerge 1975; Linsley 1937; Linsley & MacSwain 1956 and 1958; MacSwain 1945; Michener *et al.* 1955; Michener & Rettenmeyer 1956; Rozen 1968 and 1973; Stephen 1966*a* and 1966*b;* Thorp & Stage 1968; Youssef & Bohart 1968), and these provide us with a framework for generalizations about the natural history of the genus.

The purpose of this study is to describe the biologies of *Andrena (Melandrena) regularis* Malloch and *A. (M.) carlini* Cockerell with comparisons between the two species and between these and other members of the genus. The study began in Brownfield Woods, northeast of Urbana, Illinois, but was largely undertaken in Mohannes blueberry field, 5 miles west of St. Stephen, New Brunswick, Canada. Some data were also obtained in Busey Woods, in north Urbana, and from museum collections in the care of John K. Bouseman and Wallace E. LaBerge while a revision of the subgenus *Melandrena* was in progress. Laboratory work was done at the Illinois Natural History Survey.

Before the present study only scattered information was available regarding the biologies of *A. regularis* and *A. carlini.* Packard (1868) briefly described the burrow of *regularis* (determined as *Andrena vicina*) and outlined the temporal developmental sequence from egg to pupa. Packard (1897) also provided a brief description of the larva of *regularis* (determined as *vicina).* Atwood (1933) studied the Apoidea of Nova Scotia visiting the apple bloom and provided a short description of the nest structure of *carlini.* Boulanger *et al.* (1967) initiated studies on the native Apoidea associated with low-bush blueberries in southern New Brunswick and Maine. Both *carlini* and *regularis* were found in abundance in fields surveyed, and *regularis* was considered one of the most important native pollinators of blueberries. Some information on seasonal appearance, nesting habits, and flower relationships was given for *regularis.* Osgood (1972) noted that several species of native blueberry pollinators in Maine, including *carlini* and *regularis,* chose particular sites in which to nest, and he delineated soil and physical characteristics of areas where extensive nesting occurred. Kevan (1977, and unpublished) noted the decimating effect of Fenitrothion (an organophosphate insecticide) on wild bee populations and the subsequent reduction in blueberry yield. Kevan considered both *regularis* and *carlini* important native blueberry pollinators (among other species) adversely affected by Fenitrothion application. Lastly, Bouseman & LaBerge (unpublished) have recently revised and characterized the subgenus *Melandrena,* providing a list of the member species in the Western Hemisphere and details of their distribution and floral preferences.

Many people are to be thanked for their help with several aspects of this project. Foremost among these are William and Cole Bridges, who kindly allowed study and excavations in their blueberry fields in New Brunswick and the use of their facilities during the growing seasons of 1976 and 1977. Others whose help enhanced the quality of the work are: John K. Bouseman, Mary Fischer, Peter G. Kevan, Bruce Pendrel, Kenneth Robertson, and Donald W. Webb. Thanks are also due to George C. Steyskal of the U.S. Museum of Natural History, Washington, D.C., for his prompt identification of the anthomyiid fly found at the nest sites. We wish to thank Bernice Sweeney, Illinois Natural History Survey, for her assistance in typing, Lloyd LeMere, Survey Technical Illustrator, for designing the cover, Larry S. Farlow, Survey Technical Photographer, for aid in preparing the illustrations, and Shirley McClellan, Survey Assistant Technical Editor, for final editing.

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MATERIALS AND METHODS

Photographs were taken in 1976 with a 135 mm Minolta SR1 camera and a 55 mm Asahi Pentax camera by Peter Kevan and Bruce Pendrel, respectively. Photographs in 1977 were taken with a Nikon FT2 camera and a f2.8 Vivitar macro lens. Field

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temperatures were obtained with a shaded Celsius thermometer hanging about 1 foot from the surface of nest entrances.

In 1976 *A. regularis* burrows were marked with 3-inch brass paper fasteners and numbered consecutively as it became evident that the burrows contained actively nesting females. *A. carlini* burrows were marked randomly with brass fasteners. In 1977, *regularis* females were marked on the thorax with Aero Glass Dopa paint and fasteners were marked with the same color. The color code used was that described by Davis & LaBerge (1975). Burrows of *carlini* were marked again randomly with uncolored brass fasteners.

Burrows were poured with plaster of paris and excavated using shovel, pliers to cut through roots when necessary, camel-hair brushes, a 1–inch paint brush and a pocket knife. Burrow and cell measurements were made with a divider and a ruler in millimeters. Plastic vials were used to transport excavated cells and their contents. In 1976 larvae and eggs were stored in 70-percent ethyl alcohol. Adult females captured early in the season were stored in 70-percent alcohol prior to dissection; those captured later in the season were pinned. In 1977, eggs, larvae and females for dissection were all stored in Kahle's solution for 24 hours and then placed in 70-percent alcohol.

Pollen was obtained from burrow cells, the stomach contents of predefecating larvae, the scopa of female bees, and the forage plants themselves. In preparation for analysis, pollen was placed in glycerin jelly, stained with basic fuchsin, and mounted on slides (Thorp 1969; Davis & LaBerge 1975). Native forage plants were collected, pressed and brought back to the laboratory for determination.

For morphological studies, larvae were cleared in lactophenol, washed in distilled water and a 1-percent hydrochloric acid solution, and stained with acid fuchsin (Davis & LaBerge 1975). Measurements for line drawings were taken with an ocular micrometer of an M5 Wild dissecting microscope. The fine structure of the head capsule, mandibles and spiracles were further examined with a scanning electron microscope. Mandibles and head capsules were prepared using the critical paint method of drying. Specimens were dehydrated in an alcohol and a freon series and then placed in a Bomar SPC 900 critical paint apparatus. Following critical paint drying, specimens were mounted on aluminum plates, placed in a vacuum evaporator, and coated with carbon and a gold paladium alloy. Scanning electron micrographs were taken with a JEOL JSM-U3 scanning electron microscope by Daniel Ghiselli and Helen Sandburg at the University of Illinois.

Nests of *A. carlini* 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, Illinois. The woods is located just east of 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 owned by the University of Illinois and is adequately described by Davis & LaBerge (1975).

The Mohannes blueberry field site (Fig. 1) of nests of both *A. carlini* and *A. regularis,* located 5 miles west of St. Stephen, New Brunswick, Canada, is owned and operated by Bridges Bros. Ltd., commercial blueberry farmers in southern New Brunswick and Maine. It is located on upland, abandoned farmland and is managed primarily by alternate burning of one-half of the field each spring (Kevan, unpublished). The field is stony with large outcrops and the topography varied, ranging from flat to gently sloping. The soil is well-drained, sandy and developed on glacial till. It consists primarily of Carlton shaly loam (gravelly loam or clay) and Georgetown gravelly sandy loam (coarse gravel deposits that occur in the form of outwashes, kanes and eskers). Such characteristics are common to the low-bush blueberry soil of Charlotte County, New Brunswick (Boulanger *et al.* 1967). The blueberry species in this field were *Vaccinium angustifolium* Art. and *V. myrtilloides* Michx.

In the following account our observations on *A. regularis* will be described first, followed by the observations on *A. carlini* and discussion and comparisons with other species of *Andrena.* As much as is possible, the account of the biology of *carlini* will be compared with that of *regularis,* so that similarities of behavior and morphology need not be repeated.

Whenever possible, each measurement is given as a mean, followed by its standard error in the conventional statistical manner.

ANDRENA (MELANDRENA) REGULARIS MALLOCH

Andrena regularis ranges throughout the Boreal and Transition Zones from western British Columbia to New Brunswick in Canada south into Pennsylvania, northern Ohio, Wisconsin and northern Minnesota in the United States. It has been collected from 6 April through 30 June and is relatively polylectic in its known floral visits (Bouseman & LaBerge unpublished).

Nest Site Characteristics

The nest site of *A. regularis* studied was located on a small, gently sloping mound about 3.1 meters from a roadside edge (Fig. 1). An aggregation of 36 nests was found within a 1.2 by 0.9 meter area with a majority of the nests clustered on the high-

Fig. 1.—The nesting mound of *Andrena regularis* in Mohannes blueberry field, New Brunswick, in May 1976.

est portion of the mound, commonly in groups of two or three with some burrow entrances only 2.5 cm apart (Fig. 2). Additional nests were scattered along the periphery of the nesting area.

The mound was covered with burned stalks of lowbush blueberries *(Vaccinium angustifolium* and *V. myrtilloides),* lichens, some grass, leaves and twigs. Nest entrances were not obscured by the debris, but remained open and visible. The cover gradually thinned peripherally, changing from moderately dense to extremely sparse. Burrow entrances were densest in the area covered by burned *Vaccinium* stalks, with only a few entrances distributed in the sparsely covered peripheral areas. By the end of the season, here considered to be the end of the blueberry bloom and cessation of bee activity in late June, the area was covered by new blueberry shoots which appeared at the base of the burned stalks (Fig. 3 and 4).

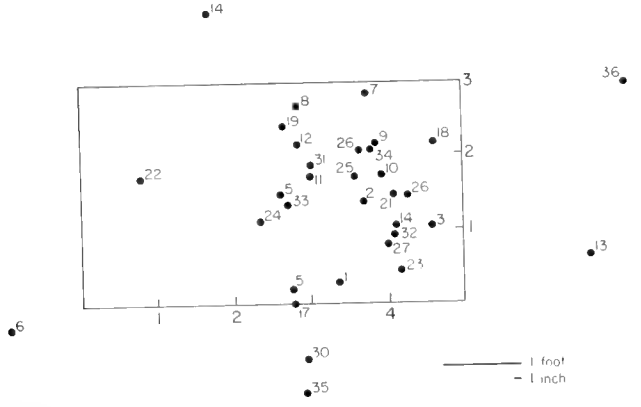


Fig. 2.—Diagram of the *Andrena regularis* nest aggregation showing locations of active burrows (1976).

Emergence, Prenesting and Mating Behavior

Upon discovery of the nest site on 26 May 1976, nesting was well under way and no prenesting activities were observed. On 12 May 1977, males and females were found crawling on the surface of the nest site. Blueberry bloom had not yet started, and closed buds were present on blueberry stalks throughout the field. Inclement weather halted bee activity from 13 May through 16 May, and burrows were excavated in order to retrieve *A. regularis* females. Specimens obtained in this manner were later dissected and found to contain sperm in the spermathecae. This indicated that copulation had occurred on or before 12 May 1977.

On 16 May a male and female were captured with a screen cone from a burrow that had been marked the previous season (Fig. 3). Both specimens

Fig. 3—Burrows of *Andrena regularis* marked with brass paper fasteners. Note the vegetation and proximity of some burrows (1976).

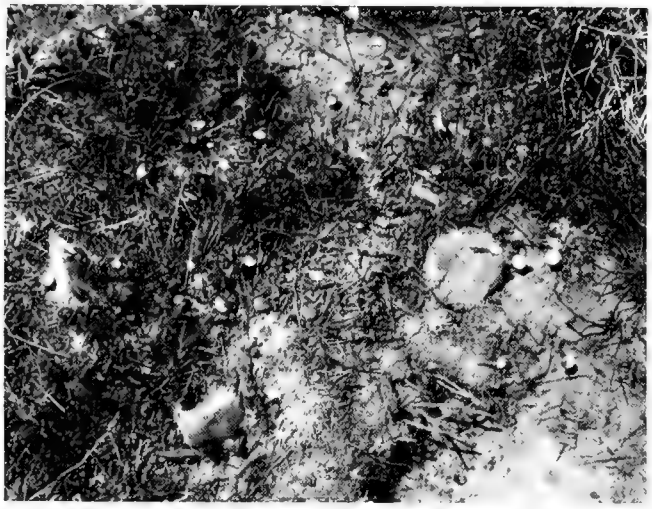


Fig. 4.—Burrows of *Andrena regularis* marked with color-coded brass paper fasteners. Note the wire cones used to capture females as they emerge from the burrows (1977).

were thought to be first emergers and the female was later found to have no sperm in her spermatheca.

Males were noted patrolling among blueberry stalks on May 16, and were also seen pollen and nectar feeding on blueberry blooms that had begun to open on 17 May. Females were also seen alighting on blooming blueberry vegetation, but no pollen collecting was observed. The females seemed to be pollen and nectar feeding, as were the males.

By 20 May the males were absent from the field and females were noted bringing pollen back to new burrows located on the nesting mound. Although more patches of blueberry were coming into bloom, the majority of plants were still in bud. Pollen sampling from females indicated that they were obtaining pollen from rosaceous plants located across the road from the blueberry field. Although dissections indicated that females had copulated as early as 12 May, and both sexes were observed patrolling blueberry stalks, copulation was not seen in the field.

Nest Architecture

Extensive excavation of *A. regularis* nests began 17 June 1976, when blueberry bloom was nearly gone and active foraging and provisioning of nests had nearly stopped. Active females in the field at this time exhibited characteristic signs of old age—confused behavior, frayed wings and loss of thoracic hair. During excavation females were often found face up in burrows, 8 to 15 cm below the surface. Females thus caught in plaster were often alive, but also exhibited signs of old age (Michener *et al.* 1955). Burrows without females in them were encountered and either were followed to the final cell (two nests) or were lost at shallow depth (ca. 10 cm). In the two nests followed to an end cell, this cell was not completely provisioned. This evidence suggests that upon completion of provisioning, the female fills in the main burrow with earth, leaving about 10 cm of the burrow open, and that the old female often remains in the 10 cm of burrow left open.

In Burrows excavated earlier in the season the deepest cell usually was incompletely provisioned. For instance, a burrow dug on 8 June 1976 contained a small larva immersed in a liquid pollen mass. The other cell at the end of the main shaft contained a small, ill-formed, irregular pellet of pollen. In other excavations, larvae in later stages of development were usually found closer to the surface than those in earlier stages or incompletely provisioned cells.

Excavation of nests in 1977 began early in the season (20–27 May). Females were captured with small wire cones placed over the burrow entrance before excavating a nest. Information was similar to that of 1976. If only one cell was found in a burrow, it was invariably located at the bottom of the main shaft and contained a roughly formed pellet of pollen and no laterals were observed. If two cells were found, the completed cell was slightly shallower in depth, was fully provisioned, contained an egg, was capped, and the burrow leading to the cell was closely packed with soil. The main shaft of the burrow was extended to a deeper level and the second cell was found at the end of this shaft. Occasionally roots and/or stones displaced the main burrow so that the second cell was located at about the same depth as the first.

Information from 1976 and 1977 indicate that *A. regularis* nests had the following characteristics (Fig. 5 and 6). Nests were 15–19 cm in depth and burrow diameter ranged from 7.5 to 9.0 mm. Main burrows were simple, unbranched and vertical to sloping at 45 degrees from the surface. Alterations in direction caused by stones and large roots were evident. Cells were often separated from such rocks only by a thin wall of earth consolidated by secretions of the female. Such secretions permeated the soil for

a depth of 1 mm, making it much harder than the surrounding earth. The inner surfaces of the cells were shiny and occasionally covered by scattered droplets of liquid.

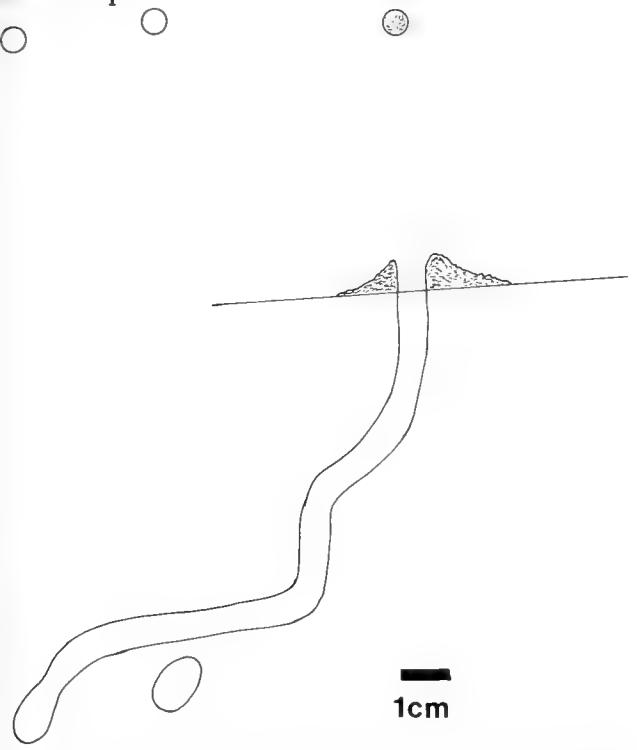


Fig. 5.—Diagram of a typical nest of *Andrena regularis* found early in the season. The open circles at the top of the figure indicate position of cells in relation to the nest entrance (the darkened circle).

Cells were found from 10–22 cm below the surface and were slanted at about 45 degrees from the vertical. Each cell was urn-shaped, averaging 14.5 ± 0.23 mm in length (N = 16), 9.0 ± 0.29 mm in width (N = 21) and 5.6 ± 0.22 mm at the narrowed neck leading to the burrow. Cells were plugged with grains of soil smoothed into the narrowed neck and arranged in a circular pattern. Four to five cells were usually found per burrow and cells were randomly placed around the main burrow. Cells were always constructed at the end of the main shaft as it was extended laterally and/or vertically. Upon cell completion 3.0–8.0 cm of the burrow was filled with soil.

Behavior at the Nest

Nest construction is probably begun soon after emergence by females of *A. regularis*. Burrows were evident on 26 May 1976 and on 12 May 1977. Burrows were located on gently sloping, well-drained areas. Digging typically began vertically on bare soil surrounded by vegetation or covered with lichens, but, where the slope of the surface was great, digging began horizontal to the surface.

On 29 May 1976, at about 1500 hours, a pollen-laden female was observed searching for a nest site and beginning a new burrow. She initially dug a shallow burrow (5–6 mm deep), then abandoned the site and began digging a short distance away. The female dug head first, breaking small, irregularly shaped pieces of earth with her mandibles. The earth was pushed backwards with the prothoracic legs, be-

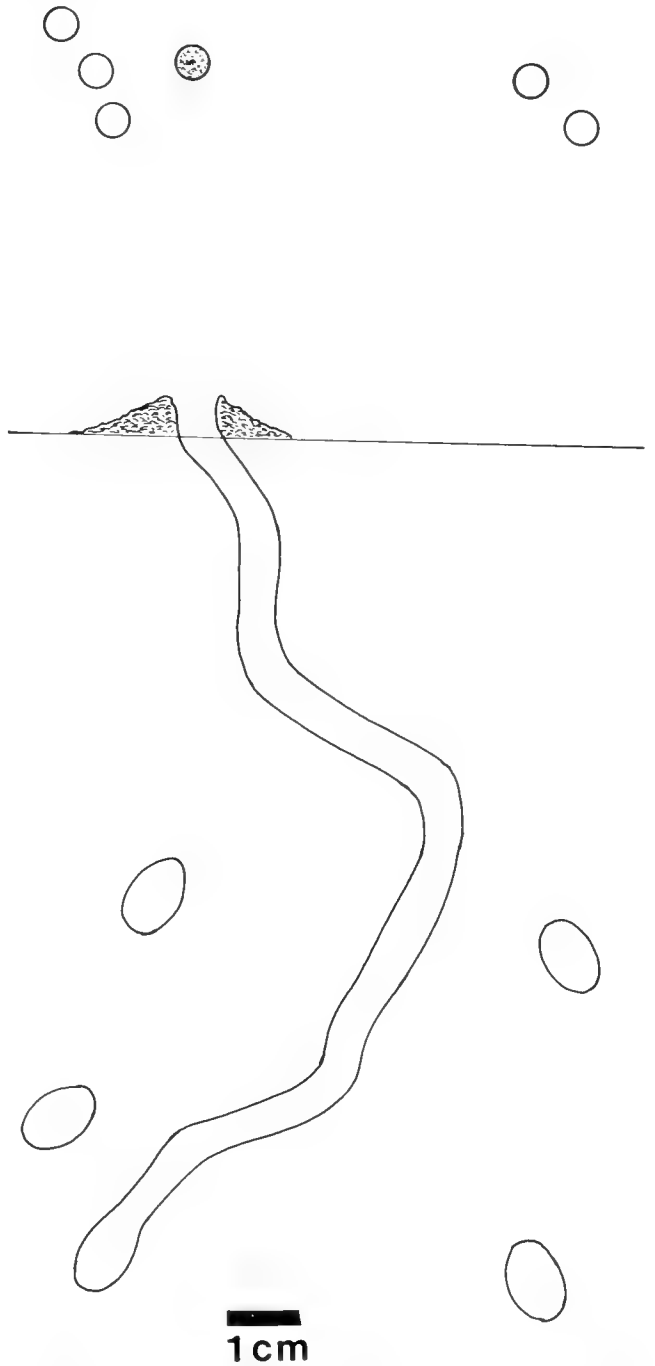


Fig. 6.—Diagram of a typical *Andrena regularis* nest found late in the season. Open circles at the top of the figure indicate positions of cells in relation to the nest entrance (darkened circle).

tween the mesothoracic and the pollen-laden, metathoracic legs. The mesothoracic and metathoracic legs were not seen to assist in either digging or pushing the earth back. As digging progressed, the female's body moved in both clockwise and counterclockwise circular motions around the perimeter of the burrow entrance. Her abdomen flicked out small pellets of earth as she dug deeper; the pygidial plate visibly pumping against the sides of the cavity. Her abdomen had completely disappeared, when the female backed out of the nest and began grooming of face and antennae with her prothoracic legs. She was disturbed by a gust of wind which blew her out of the immediate area, but she returned in a moment, relocated the excavation site and crawled into the burrow entrance. Earth was periodically heaved upward at the entrance of the burrow, some spilling out and around the entrance and some falling back into the burrow. The female at this time was entirely covered by the earth and was inside of the burrow. The heaving motion of the earthen pellets was probably due to the pushing thrusts of the abdomen and the backward action of the prothoracic legs as observed earlier.

The female had taken about 20 minutes to reach this point. She then backed out of the burrow through the loose earth, antennated the surface, hovered over the nest and did a characteristic zigzag orientation flight. She hovered over the entrance once again, landed and recommenced digging. This sequence of activity lasted about 4 minutes.

The female remained visible for about 4 minutes pushing back earth from the entrance in a clockwise-counterclockwise circular pattern until she once again disappeared beneath the soil. After about 3 minutes, the female resurfaced head first, turned around at the entrance and disappeared again, head first into the burrow. The female was not seen again that day, but on 30 May she was actively foraging and returning to the new burrow with pollen. The entrance at this time was somewhat obscured by the fresh tumulus through which the female dug.

A concentric mound of earth forms around the entrance of a burrow in the process of being excavated. This tumulus sometimes obscures the burrow entrance, but this condition seems to be temporary. The burrow entrances of *A. regularis* were found to be mostly open and quite visible. The tumuli varied in size (3.4–4.0 cm in width and 1.0–1.5 cm in height) and were often absent. Wind and rain generally obliterated tumuli soon after they were formed.

Burrows of *A. regularis* were left open during periods of daily foraging activity. After cessation of foraging, the female disappears into the burrow and may plug the entrance with particles of freshly dug soil (Fig. 7). At no time were all entrances of the burrows in the nest aggregation plugged with soil. Observations further indicated that definite trends in

Fig. 7.—Photo of a plugged nest entrance of *Andrena regularis* (23 May 1977).

daily nest-plugging behavior existed. For example, plugging occurred anytime from 1100 hours to 1500 hours in the afternoon; though spot checks of the nest aggregation indicated that plugging continued well into the evening (i.e., 1945 hours). Females usually remained in the burrow and did not recommence foraging during the day in which the entrance was plugged. Females in burrows plugged early (i.e., 1100 to about 1430 hours) departed earlier for foraging on the following day than those plugging late in the day. Females leaving burrows unplugged overnight, generally began plugging activity earlier on the next day than those whose nests had been plugged the night before.

From such observations it is likely that plugging occurs when *A. regularis* has collected a volume of pollen sufficient to provision a cell. Soil pushed to the surface and plugging the entrance are due, thus, to the construction of a new cell or further burrow excavation or both. For example, on 28 May 1976, a female began plugging her nest at 1300 hours. Although activity seemed to have ceased, more soil was observed pushed toward the entrance at 1703 hours, as if the female had resumed excavation. On 29 May 1976, another female arrived at her burrow at 1232 hours and plugging was evident a few mm below the surface at 1234 hours. This entrance was observed carefully and particles of fresh earth were observed

being thrust upward in loads of varying volumes every 12–30 seconds (average 19 seconds). The longer periods of time were followed by larger volumes of earth pushed upwards. Sixteen loads of dirt were counted before activity ceased at 1238 hours, a total of 6 minutes. Similar observations were recorded for other females in the aggregation.

Nests were difficult to spot in Mohannes blueberry field because of the surrounding blueberry vegetation and debris. Nests were located by investigators as they sat quietly and closely watched a portion of the burned field. Females were observed landing on the lip of a burrow entrance, pausing momentarily and entering. Often no hesitation in locating the burrow was observed; females were able to fly directly to it. Sometimes, however, a female experienced difficulty in returning to her burrow, especially if the nest entrance was obscured with debris. On 6 June 1976, a pollen-carrying female twice attempted to locate a nest covered with earth and bits of grass. She hovered over the nest, landed near the entrance only to fly up and hover once more before flying a zigzag orientation pattern over the entire area. After landing near the nest a third time, she dug her way into the burrow.

Similar observations were made in 1977 when females initially began foraging. Upon return from the field, pollen-laden females would perform an orientation pattern around the nest aggregation, the zigzag pattern becoming smaller until the female hovered over the burrow entrance. The hovering lasted a few seconds until the female landed near the lip of the entrance, paused momentarily and entered. Since females and their corresponding nest markers were color coded with Dopa aeroglass paint, it was further noted that females consistently entered the same burrow in the aggregation.

Females of *A. regularis* take 64.2 $\pm$ 5.64 mins. (N = 65) to make a pollen collecting trip. Pollen-laden bees entered the burrow head first and remained in the nest for an average of 30.9 $\pm$ 2.26 mins. (N = 72). While in the burrow females sometimes remained a few mm below the entrance, the head, and sometimes the head and thorax visible (Fig. 8). Sudden movement, or a shadow falling across the entrance, disturbed the female, causing her to back down into the burrow. After a few minutes, the bee reappeared at the surface and seemed to be peering at the observer. This would occur midday when females were actively foraging. Such behavior was especially noticeable when *regularis* females left the burrow for the first foraging trip of the day. The female in emerging head first often antennated the burrow wall near the entrance. One female periodically moved towards and away from the entrance, often poking head and thorax outside of the opening, for a total of 1 hour, at which time she left the burrow for her first foraging trip.

Fig. 8.—Characteristic pose of an *Andrena regularis* female at the burrow entrance before departing on a foraging trip (27 May 1977).

Orientation flights characteristically preceeded the first foraging excursion of the day. The female would crawl out of the nest, hover over the burrow for a few seconds, fly straight up and momentarily hover 10–12 cm above the burrow. She then circled the aggregation in an irregular zigzag pattern which became larger until it encompassed the entire area of nests, and she left the pattern to disappear from view. On subsequent foraging trips during the day, females rarely executed an orientation flight upon departure. If the nest entrance became obscured while the bees were foraging, nest entrances were located after some difficulty and the female executed another orientation flight upon leaving the nest.

Occasionally ants disturbed the bees. In one instance a female entered the burrow only to immediately back out and take flight. An ant was seen at the burrow entrance. Two minutes later the female returned, but was once again disturbed by the ant and departed. The ant soon left and after about 5 minutes the female returned, entered and plugged the burrow for the evening. Similarly, a pollen-laden female was chased by two ants as she attempted to return to her burrow. She hovered over the nest, almost entering, when two ants at the entrance grabbed her right foreleg. The female emitted a distinct buzzing sound, pulled away from the ants and flew away. She returned to the burrow 14 minutes later and entered without incident, but an ant was observed coming from the nest directly after the female entered.

Occasionally *A. regularis* returned to their burrows with little or no pollen. This was more common towards the end of the season, prior to 16 June. At

this time activity around the nest site had diminished. Though some females were found in burrows while excavating them, most burrows had been abandoned. We believe that most females abandon their burrows after completing them. The behavior of the bees in the field at this time seemed disorientated and females flew about aimlessly, unable to locate burrows. Occasionally, bees clung to blueberry stalks or landed and walked on the ground, stopping to groom face and antennae.

Foraging and Provisioning of Cells

Much of the pollen collected by *A. regularis* in Mohannes field was that of low-bush blueberries *(Vaccinium* spp.). However, pollen found in the cells of developing larvae included that of the family Rosaceae. During the period of 20–27 May 1977, sampling indicated that *regularis* females foraged on apples *(Malus* sp.), fire cherry *(Prunus pennsylvanicus),* choke berry *(Aronia arbutifolia),* choke cherry *(Prunus virginiana),* shadbush *(Amelanchier* sp.), and hawthorn *(Crataegus* sp.), as these plants came into bloom in the vicinity of Mohannes field. Blueberry plants were not yet in bloom and *regularis* females used these other pollen sources to initiate nesting.

Incompletely provisioned cells contained a rough, spherical, ill-formed pellet of pollen (Fig. 9). Completely provisioned cells contained moist, subspherical, somewhat flattened, pollen masses to which nectar had obviously been added. The dorsal lip of the mass (relative to the cell plug) was rounded and thickened, and the center portion depressed. The overall shape of the mass resembled a thickened red-blood platelet (Fig. 10). It seemed as if the female had formed a spherical pollen mass and then flattened and molded the surface with her abdomen as she laid an egg.

Fig. 9.—The rough, spherical, pollen pellet found in an incompletely provisioned cell of *Andrena regularis.*

Fig. 10.—A completed cell of *Andrena regularis.* Note the somewhat depressed, flattened, pollen mass. The egg is positioned upright, one end embedded in the depressed center of the pollen mass (the sphere to the left of the cell is the head of a brass paper fastener).

In the 1976 season pollen consistency within the cells of the same burrow varied. In some cells provisions appeared liquidy, so much so that young larvae were immersed in the mass with only the dorsal portion of the body visible. In other cells pollen was dry and cakey, and a larvae removed from such a cell left indentations of its body across the pollen surface (Fig. 11). In either case, the pollen was distinctly yellow and did not change color as it was consumed by the larvae.

Females were observed leaving their burrows from 0830–1100 hours. No bees were observed bringing pollen loads back to the burrow before 0930 hours. It is likely, however, that some females began foraging before 0830 hours, as temperatures were often as high as seemed necessary for foraging. Plugging occurred from early morning to early evening and females ceased foraging for the day after plugging occurred. Many bees foraged until sunset, although some females returned and plugged burrows as early as 1100 hours and others plugged burrows between 1400 and 1800 hours. The time expended per foraging trip ranged from 23 to 272 minutes. Time spent in burrows between foraging trips ranged from 10 to 97 minutes.

Developmental Observations

In 1977 *A. regularis* began nesting in Mohannes field shortly before or on 22 May. Nests excavated from 15 May–19 May were blind burrows without cells. By 20 May females were observed returning to burrows with pollen and burrows excavated from 21 May through 27 May contained one cell with an egg. Often an incomplete cell, containing a pellet of pollen, was found at the end of the burrow. First

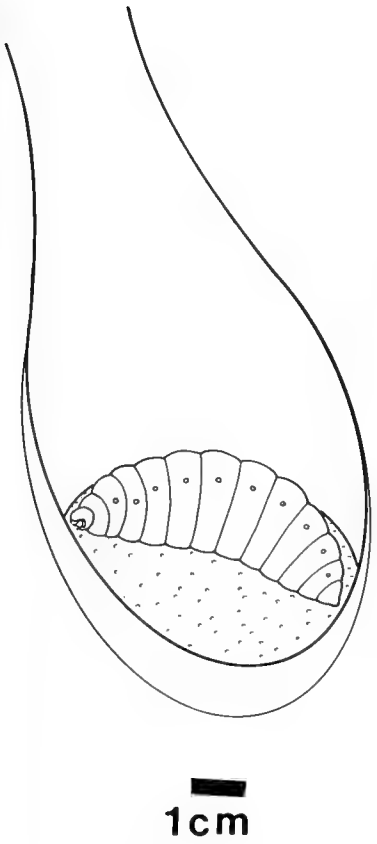
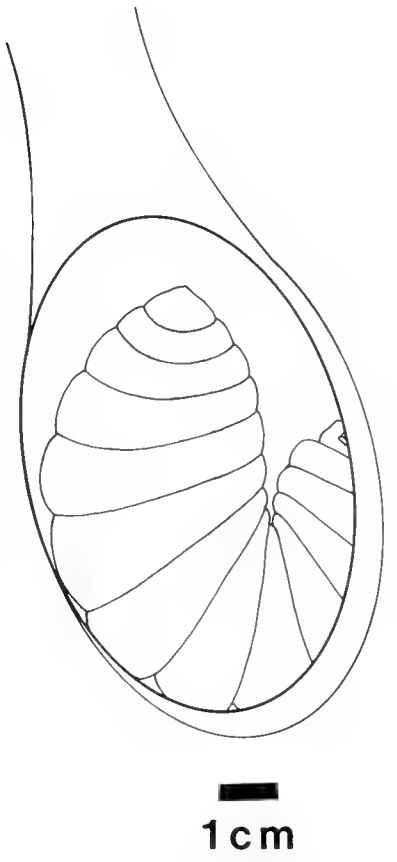


Fig. 11.—Diagram (left) showing a young larva of *Andrena regularis* positioned across a cakey, dry, pollen mass. *Andrena carlini* larvae are positioned in the same manner.

Fig. 12.—Diagram (right) of an almost mature larva of *Andrena regularis* positioned in the cell. Note the small amount of pollen at the bottom of the cell. *Andrena carlini* were found similarly positioned.



instar larvae were not found in any nest up to the time observations were terminated on 27 May 1977.

In 1976 burrows excavated from 17 June through 22 June contained larvae in various stages of development. Some larvae had consumed one-half to three-fourths of the provisions; others had consumed the provisions completely and filled the entire cell. Fieldwork terminated on 22 June 1976, and no nests were found to contain postdefecating larvae.

Larvae were found almost immersed in a liquid pollen mass in some cells. Other larvae appeared to be on the surface of a cakey pollen mass and consumed pollen directly beneath their mouthparts. Larvae encircled the pollen as they fed, until a small amount remained beneath the ventral surface of the body. Large mature larvae appeared to be positioned head down in the cell (Fig. 12).

Description and Development of the Ovary

The ovaries of *A. regularis* females differ from those of most *Andrena* now known in that they are formed into a single, fused, median organ in which six or seven ovarioles are visible. Paired lateral oviducts lead to a median genital chamber. The gonopore opens to the exterior on the posterior ventral surface of the genital chamber. Dufour's gland appears large and convoluted and shares the gonopore opening to the exterior. The spermatheca is located on the posterior dorsal surface of the genital chamber slightly posterior to the gonopore (Fig. 13).

The ovaries of two females of *A. regularis* captured at their burrows on 15 and 16 May 1977, contained follicles that were beginning to mature (Fig. 13*A* and *B*). The spermathecae of both contained sperm and the crop and midgut contained pollen. A third female was captured on 16 May 1977, from a screen cone placed over a marked nest site from the previous season. The ovary of this female was small, the follicles immature, the spermatheca contained no sperm, and the crop and midgut contained no pollen (Fig. 13*C*). The condition of this female indicated that it had just emerged, and she had not had time to feed or to copulate. A fourth female, captured on 21 May 1977, had ovaries in the condition of the first two females described above (Fig. 13*D*). On 23 May 1977, a female was captured and upon dissection was found to contain an ovary with two follicles enlarged and egglike in appearance (Fig. 13*E*), suggesting that the female was about to begin nesting.

In the 1976 season the earliest females captured and dissected were taken on 28 and 29 May. The female of 28 May had an ovary with follicles just

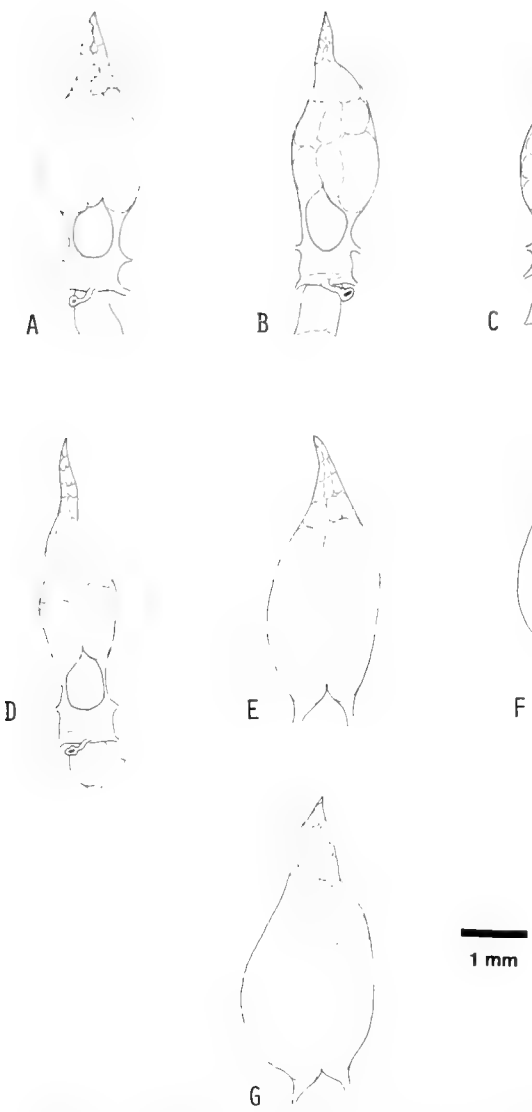


Fig. 13.—Drawings of ovaries (dorsal view) of *Andrena regularis* showing ovarian development. *A*. Female captured from burrow, 15 May 1977. *B*. Female captured from burrow, 16 May 1977. *C*. Newly emerged female taken from burrow, 16 May 1977. *D*. Female captured from burrow, 21 May 1977. *E*. Female captured from burrow, 23 May 1977. *F*. Female captured foraging, 28 May 1976. *G*. Female captured foraging, 29 May 1976.

beginning to mature (Fig. 13*F*), and the female of 29 May had enlarged, egglike follicles (Fig. 13*G*). In both cases the spermathecae contained sperm and the crop and midgut contained pollen. All females captured after 28 May had mature ovaries.

The Egg

The egg of *A. regularis* was white, slightly bowed and stood upright in the center of the pollen mass (Fig. 10). Only the distal end of the egg (relative to the cell plug) was embedded in the pollen, and it was noted that this end was slightly larger than the proximal end and rounded in shape. Eggs were 3.31 ± 0.079 mm in width ($N = 6$) and 9.92 ± 0.06 mm in length ($N = 6$).

Predefecating Larva

Body: (Fig. 14). C-shaped, about 10 mm long, mm wide in lateral view; postcephalic segments 1–rounded in profile, segment 3 divided dorsally b distinct furrow; segments 4–10 rectangular in profile intersegmental furrows distinct; integument smooth lacking setae and spicules; anal opening apicomedia on terminal segment.

Head: (Fig. 14 and 15). As in *A. candida* (Yousse & Bohart 1968) except as follows: genal area wit sparse setae; labrum with dense setae, thickened a

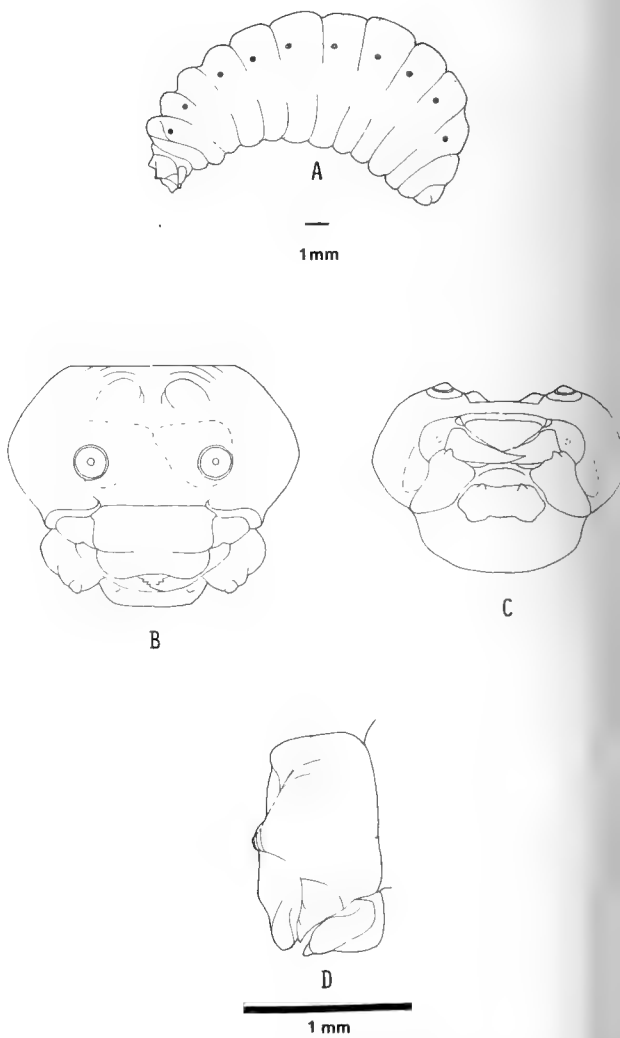


Fig. 14.—Drawings of the predefecating larva of *Andre regularis*. *A*. Lateral view of larva. *B*. Frontal view of he capsule. *C*. Inferior view of head capsule. *D*. Lateral view head capsule.

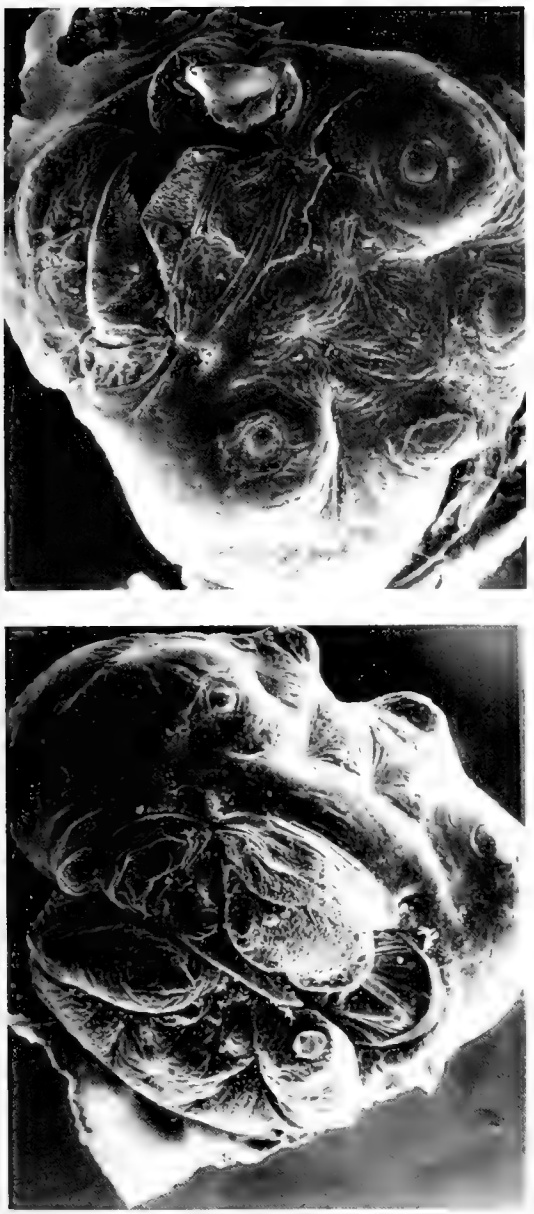


Fig. 15.—Electron microscope photos of the head of the pre-defecating larva of *Andrena regularis* showing the head in two views.

edge; maxillae with moderate setae; labium with sparse setae; epistomal suture distinct, cleavage line absent; mandibles (Fig. 16) with inner apical margin irregularly serrate to base of cusp, cusp with dorsal teeth ranging in size from robust to small; maxillary palpus larger than labial palpus; salivary opening on small tubercle; prementum indistinctly separated from postmentum.

Spiracles: (Fig. 17). Dorsolateral on thoracic segments 2 and 3, abdominal segments 1–8; atrium produced above body integument, discernible ridges present internally, primary atrial opening circular with collar.

Inquilines and Parasites

The anthomyiid fly, *Leucophora fusca* Huckett, sometimes followed *A. regularis* females. If followed, the bee attempted to lose the fly and flew in an irregular zigzag pattern in the vicinity of the nest site. Occasionally a female landed and rested on vegetation, and the fly would stop as well, to resume shadowing the bee when she once again took flight. On 29 May 1976, a female arrived at the nest site shadowed by a fly. The bee entered her burrow and the fly followed, but after a moment the fly backed out and positioned itself on a nearby blueberry twig head downward toward the nest entrance. At 1310 hours the bee left the nest to resume foraging. The fly immediately darted into the nest entrance, re-emerged in about 2 seconds and flew away from the site. At 1370 hours another female was observed being shadowed by a fly. The sequence of behavior was similar, although the fly remained poised on the lateral surface of a brass-tack nest marker. It was disturbed by an ant which had crawled up the marker and become disoriented. After resting for 3 minutes on the tack surface, the fly attempted to relocate the nest opening by crawling on the ground but was unable to do so. It resumed a waiting position on a blueberry stalk and, after spotting a pollen-laden female bee returning to the nest aggregation, it left the stalk and followed the bee to its burrow entrance. In this instance the fly followed the bee directly into the burrow and remained inside for 30 seconds before re-emerging and flying away.

Two anthomyiid larvae were found in a cell of an *A. regularis* burrow on 21 June 1976. One larva was slightly larger than the other (6 mm as opposed to 5 mm) and both were immersed in the liquidy mass at the bottom of the cell. A small, second instar bee larva was found in the mass as well.

On two occasions females of *Nomada imbricata* (Anthophoridae) were observed entering burrows of *A. regularis*. Unlike the anthomyiid fly, the *Nomada* females did not follow *regularis* females to their burrow. The *Nomada* patrolled the nest site, occasionally landing on blueberry vegetation. Before entering a burrow, the *Nomada* hovered over the entrance, landed, antennated the burrow rim and then disappeared into the burrow for 15–22 minutes. Upon emergence, the *Nomada* were easily captured by a vial placed over the burrow entrance.

An unidentified fly of the family Bombyliidae was commonly seen hovering about the *A. regularis* aggregation. This fly often hovered close to the ground, creating a small depression in open, unvegetated soil with the vibrating tip of its abdomen. A small, transparent egg was subsequently deposited in the depression.

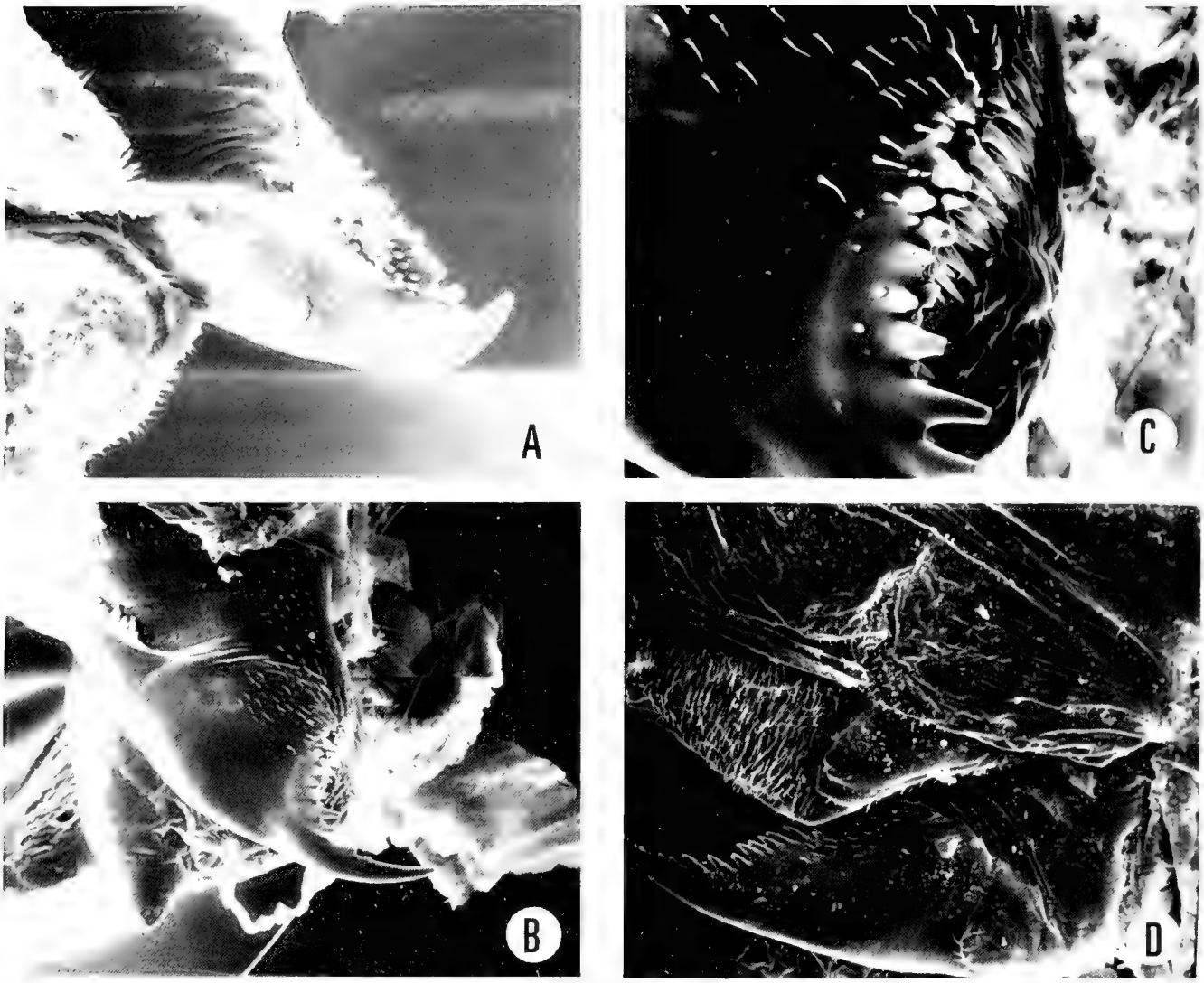


Fig. 16.—Electron scanning microscope photos of the right mandible of *Andrena regularis*. *A*. Superior surface. *B*. Outer surface showing part of the superior surface. *C*. Outer surface showing a closeup of part of the superior surface. *D*. Outer surface in relation to the labrum and clypeus.

ANDRENA (MELANDRENA) CARLINI COCKERELL

Andrena carlini ranges from Alberta and Idaho in the west to Nova Scotia and Maine in the east, and south to Georgia, Arkansas and New Mexico. It has been collected from 22 March through 26 July, but is active chiefly in April and May (Bouseman & LaBerge unpublished). It has been collected from a great many flowering plants and must be considered to be a polylectic bee.

Nest Site Characteristics

Burrows of *A. carlini* found in Brownfield Woods were located in the forest with entrances often obscured by leaves or other vegetation. Nests were isolated from one another, distances between nests ranging from a few centimeters to several meters. Female bees and their burrows were observed in Brownfield Woods for as long as 6 weeks in 1966, 1968, 1974, and 1976. Burrows were excavated several times, were found to extend vertically into the ground for 15 to 20 cm, but cells, pollen, or other signs of nesting were never found despite the fact that the females were seen entering, observed at the entrances, and taken from within the burrows.

Burrows of *A. carlini* in Mohannes blueberry field were found on elevated portions of the road and along the roadside edge (Fig. 18). Nests were isolated from one another and burrows were not usually obscured by vegetation. Some burrows were found along portions of the road covered with low grass, although entrances were easily visible. All burrows of *carlini* in Mohannes field that were excavated contained evidence of nesting activity.

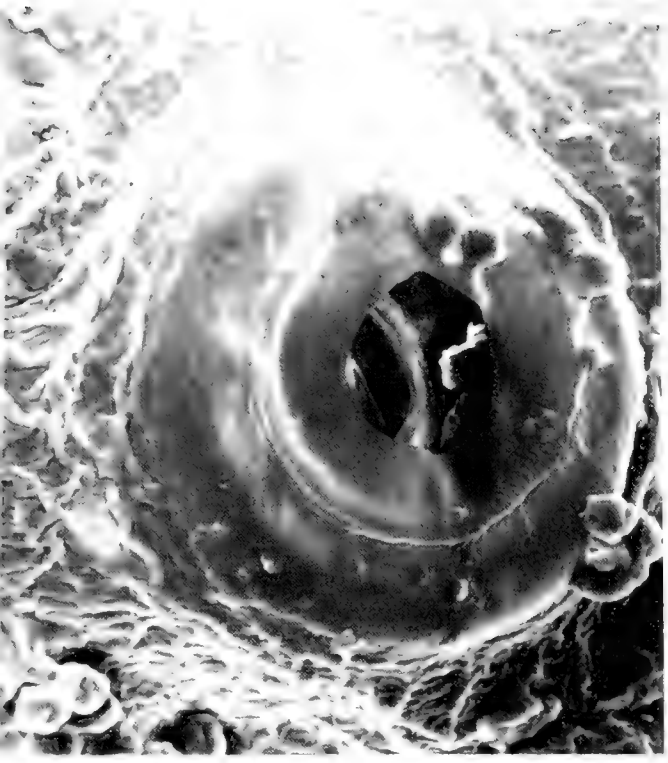


Fig. 17.—Electron scanning microscope photo of the surface of the spiracle of *Andrena regularis*.

Emergence, Prenesting and Mating Behavior

Males and females of *A. carlini* were evident foraging in Brownfield Woods, Urbana, Illinois, by 31 March 1976. Males were noted patrolling flowers *(Claytonia virginica* and *Dentaria laciniata)* probably in search of females. Females of *carlini* were not observed collecting pollen but were nectar feeding primarily from *Dentaria*, although *Claytonia* was also used. Occasionally nectar feeding was interrupted, especially in cool weather. Females would alight on leaves on the forest floor for periods of 2-3 minutes and groom themselves, often in the sunlight. After grooming, patrolling and nectar feeding would recommence. The females were strong fliers and difficult to follow, but they seemed to slow down between 1500 and 1700 hours and this is the period during which most burrows were discovered.

Foraging females of *A. carlini* were observed stripping pollen from anthers of trout lily *(Erythronium* sp.) in Brownfield Woods on 6 April 1976. An attempt was made to follow pollen-laden females to their burrows without success. Most females continued to nectar feed and pollenless females returned to burrows in the leaf litter under the forest canopy. On 3 April 1976, one female entered a burrow in the leaf litter with some pollen on her hind legs. This burrow was later excavated and proved to be

Fig. 18.—Excavating a burrow of *Andrena carlini* in May, 1977. Note the burrow is on a road, devoid of vegetation.

sterile, as were all of the burrows found in the woods. By 30 April most activity in the woods had ceased; *carlini* was rarely seen. Search of nearby areas of hard-packed soil outside of the forest canopy did not result in the discovery of any *carlini* burrows.

Males of *A. carlini* were observed nectar feeding from *Dentaria laciniata* on 30 March 1977, in Busey Woods, Urbana. On 2 April females were noted in Busey Woods and a copulating pair was observed on an open blossom of trout lily *(Erythronium* sp.). The male was positioned on top of the female with his copulatory organs placed in the female's genital opening. The pair was captured and placed in a vial where it was observed that the male had some difficulty in disengaging. Bouseman (personal communication) observed similar activity in Brownfield Woods on several occasions in the spring of 1971. On 12 April 1971, males were observed patrolling flowers of bloodroot *(Sanguinaria* sp.). Three pairs of *carlini* were observed mating on open flowers. In one case an attempted copulation was disrupted by the landing of a second male on the back of the male attempting to insert his copulatory organs into the female genital opening. On 15 April 1971, several copulatory attempts were observed but none were successful.

In Mohannes field, New Brunswick, two females were captured and dissected on 15 May 1977. Both females had sperm in their spermathecae, indicating that copulation had occurred. Males were observed patrolling blueberry stalks from 15 May through 20 May, occasionally feeding on freshly opened blueberry flowers. Similar behavior was observed for females, but by 18 May some females were observed collecting pollen on nearby strawberry bloom *(Fragaria* sp.). By 20 May, the males had disappeared from the field and females were actively bringing pollen to burrows. Sampling indicated that *carlini* females were obtaining pollen from *Fragaria virginiana, Prunus pennsylvanicus, P. virginiana, Malus* sp., *Aronia arbutifolia Crataegus* sp., and *Amelanchier* sp., all rosaceous plants, located across the road from the blueberry field. This was at a time when most of the blueberry plants were not yet in bloom.

Nest Architecture

Nest construction probably began soon after emergence of *A. carlini.* Digging behavior was not observed and it is not known whether *carlini* plugs the nest entrance with earth pellets after foraging is completed for the day as does *A. regularis.* In 1976 nests of *carlini* were excavated from 8 June through 22 June. A burrow dug on 8 June had eggs and second and third instar in cells at depths of 14.5–17.5 cm. The cell at the end of the main burrow shaft had not been provisioned. In another burrow larvae were found at depths of 16–20 cm, while the cell at the end of the shaft was unprovisioned.

In burrows dug near the end of the blueberry season (12 June through 22 June 1976), females were found face upwards in the burrows at a depth of 10 cm. Burrows were lost below this depth, suggesting that at the completion of the last cell the burrow had been plugged to a distance of about 10 cm from the surface.

Burrows of *A. carlini* were excavated early in the season in 1977 (20–27 May) at the onset of active foraging activity. If one cell was found in the burrow, it was invariably located at the end of the main shaft and contained a roughly formed pellet of pollen. If two or three cells were found, the completed cells were slightly shallower in depth, contained pollen and eggs and were capped. The portion of the burrow leading to the completed cells was filled with closely packed soil. A cell at the end of the main shaft (seemingly extended after the last cell was completed), usually slightly deeper than the completed cells, contained incomplete pollen balls or nothing at all.

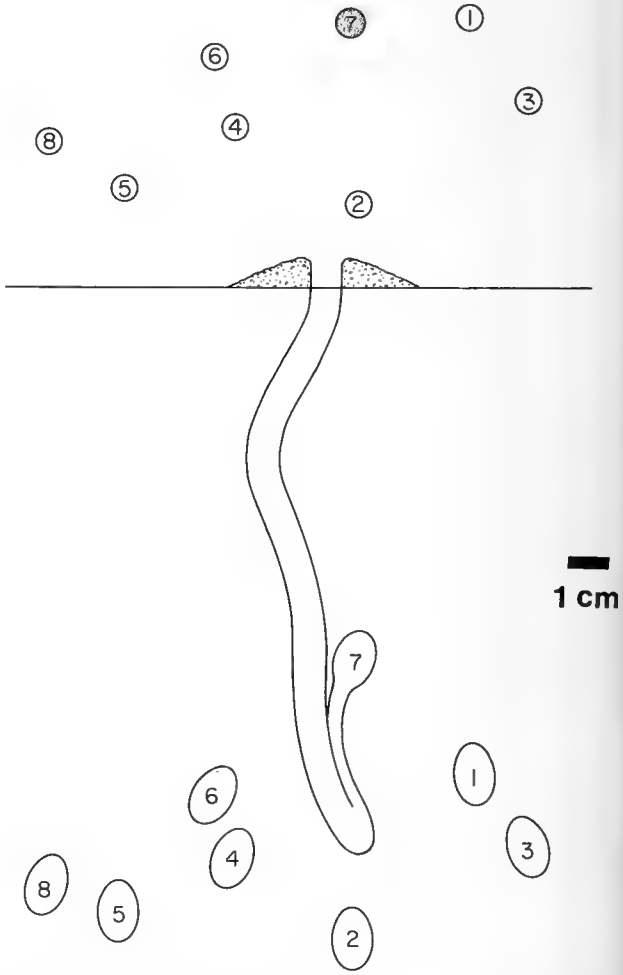


Fig. 19.—Diagram of an *Andrena carlini* burrow dug in 1976. The cells are numbered in the order of discovery. Open circles at the top of the figure indicate the random arrangement of cells in relation to the nest entrance (darkened circle).

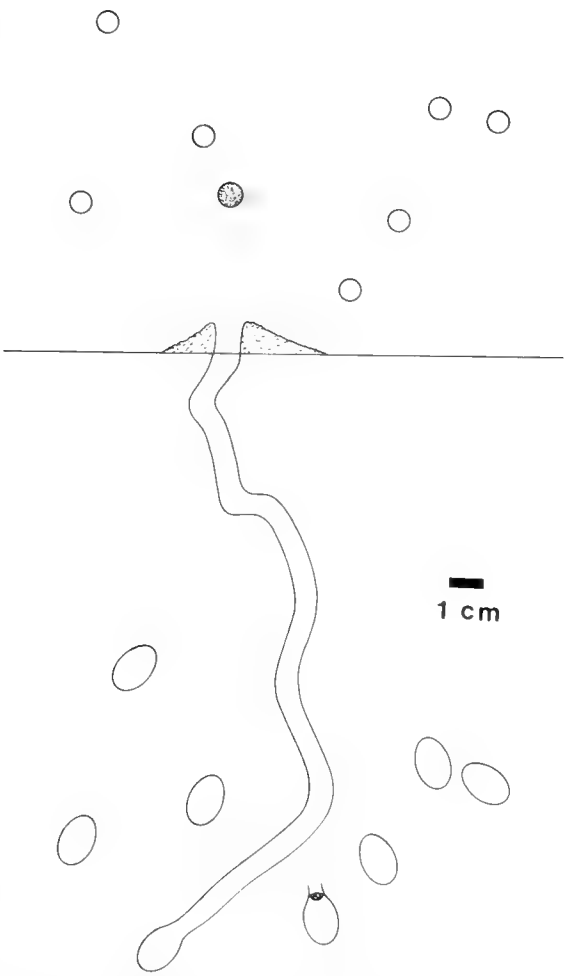


Fig. 20.—Diagram of a nest of *Andrena carlini* with the arrangement of cells indicated by open circles and the nest entrance by a darkened circle at the top of the figure (1977).

Information from both 1976 and 1977 are grouped together in the following nest descriptions (Fig. 19 and 20). Tumuli surrounded most nest entrances and ranged from 3 to 5 cm in width and 0.5–1.0 cm in height. Burrow shafts were 14–23 cm in depth, and diameters ranged from 7.5 to 9.0 mm. Main burrow shafts were simple, unbranched and vertical on flat surfaces. Along road banks, however, burrows were initially constructed horizontally before extending vertically downward. Shafts often curved to avoid obstacles. In one nest, the burrow made a sharp right angle at 15.5 cm depth, and extended slightly upward ending in a cell at a depth of 14.5 cm. Other cells of this burrow were found at depths up to 17.5 cm (Fig. 19). However, burrows usually extended vertically into the earth, ending in a single incompletely provisioned cell which was the deepest cell of that burrow (Fig. 20).

Five to eight cells were found per burrow, although one nest had only three cells. The cell wall was consolidated and the inner surface polished as in *regularis*. Cell plugs in completed cells were as described for *regularis*. Cells were found to occur from 13.5–26.0 cm in depth and ranged in position from vertical to nearly horizontal. The majority of cells were slanted downward from the burrow at an angle of 45 degrees from the horizontal. Cells were urn-shaped, averaging 14.1 $\pm$ 0.40 mm in length (N = 15), 9.4 $\pm$ 0.23 mm in greatest width (N = 16) and 5.8 $\pm$ 0.66 mm (N = 9) at the narrow neck.

Behavior at the Nest

Observations of *A. carlini* behavior in Mohannes field, New Brunswick, were not as extensive as those on *A. regularis*. On one occasion, however, it was noted that the female was able to locate, land on the lip and enter the burrow without an orientation flight.

On 6 April 1976, in Brownfield Woods, Urbana, Illinois, an *A. carlini* female was observed upon returning to a burrow to land upon a dry leaf, fly up and hover over the leaf, land on the leaf a second time, and then disappear beneath the leaf. When the leaf was removed, a burrow entrance was uncovered. In some instances in Brownfield Woods, when the burrow entrances were not obscured by leaves, the females seemed able to fly directly to the entrance.

Behavior of *A. carlini* at their nests was not observed in Mohannes field, New Brunswick. In 1976 in Brownfield Woods it was observed that females would occasionally remain in burrows, head up, a centimeter or so below the surface. They would occasionally move up to the burrow rim, antennate the surface and move back down when startled by movement of the observer or a shadow. Upon leaving the burrows, females crawled out to the narrow rim, antennated the surface, emerged and hovered over the burrow entrance, and executed an orientation flight over the area. Overcast, cool weather seemed to reduce activity of foraging females of *carlini* both in Brownfield Woods and in Mohannes field, but did not stop it altogether.

Foraging and Provisioning of Cells

In completely provisioned cells of *A. carlini* nests contained rough, spherical, ill-formed pellets of pollen. Completed cells contained moist, flattened, spherical pollen masses to which nectar had been added and they were very similar to those of *regularis*. In the season of 1976, pollen consistency within completed cells of the same burrow varied. Larvae were sometimes immersed in a liquid mass, and at other times lay on the surface of a pollen mass of cakey texture. No data were obtained concerning foraging time of *carlini*.

Developmental Observations

In 1977 *A. carlini* in the Mohannes field began

nesting activities just before or on 21 May. Nests excavated on 15 May and 18 May were blind burrows, without completed or partially completed cells present, and resembled the burrows of *carlini* found in Brownfield Woods, Urbana. Females were observed returning to burrows laden with pollen on 21 May and burrows excavated from 21 May through 27 May contained two to three cells with eggs. Only one incomplete cell was found per burrow, characteristically at the end of the main shaft and usually containing a rough, unfinished pellet of pollen. Field observations of *carlini* were terminated on 27 May and first instar larvae were not yet present in any cell.

In 1976 burrows excavated in Mohannes field from 8 June through 22 June contained eggs and larvae in various stages of development. One burrow dug on 8 June contained eggs as well as a larva that had consumed about one-fourth of its provisions. A burrow excavated on 14 June contained eggs, larvae that had consumed very little provisions and a relatively large larva which had consumed nearly all of its provisions. On 16 June a burrow contained three larvae which had eaten one-half to three-fourths of their provisions. On 22 June a burrow contained eggs as well as larvae in early stages of development.

Feeding larvae were positioned as described for *A. regularis* and this depended, as in *regularis,* upon whether the provisions were semiliquid or cakey. Large, mature larvae appeared to lie positioned head downward in the cell, as in *regularis.*

Description and Development of the Ovary

The ovaries of nesting *A. carlini* are fused medially and in all details are like those of *A. regularis* described above. Females captured in the spring of 1977 in Busey Woods and Brownfield Woods were dissected to ascertain ovary development. On 2 April, a female from Busey Woods had small, immature ovaries, although the spermatheca contained sperm and the crop and midgut were filled with pollen. Two females captured on 15 April from Busey and Brownfield Woods, respectively, had ovaries in which the follicles were mature. In particular, the female from Busey Woods appeared ready to lay eggs. Both females had sperm in their spermathecae and pollen in their crops and midguts.

In Mohannes field in 1977 several females were captured to study ovarian development (Fig. 21). Before 18 May the ovaries showed little sign of development, but on that date one female seemed about ready to lay eggs, with follicles fully expanded. No female was taken, before or after 18 May, which had not copulated, as evidenced by sperm in their spermathecae. All females captured in Mohannes field after 28 May had mature ovaries and sperm in their spermathecae.

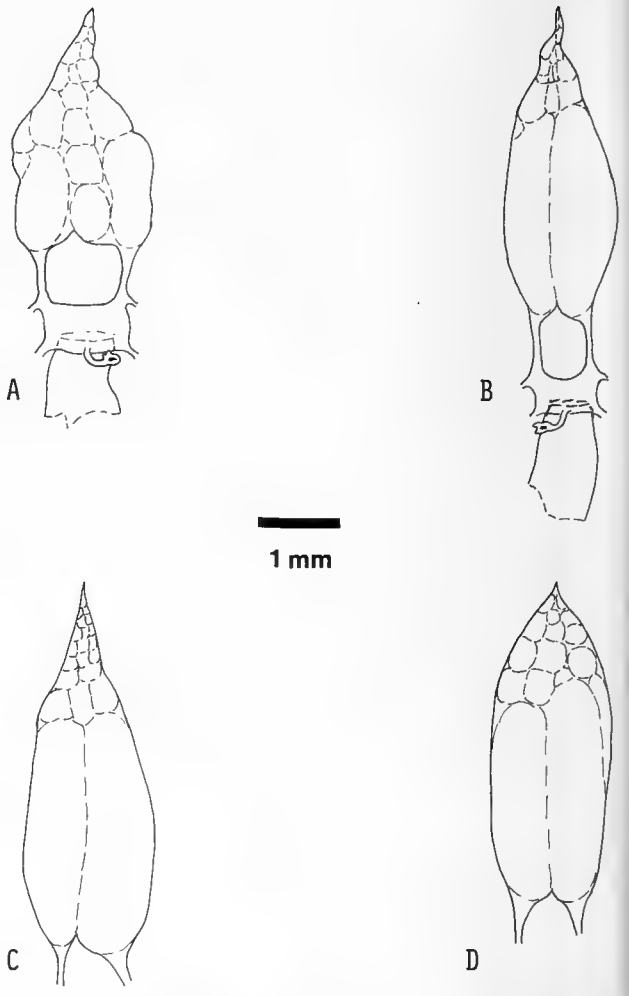


Fig. 21.—Drawings of ovaries of *Andrena carlini* captured while foraging in Mohannes blueberry field, New Brunswick. *A.* 15 May 1977. *B.* 17 May 1977. *C.* 18 May 1977. *D.* 26 May 1976.

The Egg

The egg of *A. carlini* was like that of *A. regularis* in all respects of shape and positioning in the cell. Eggs of *carlini* averaged 3.10 ± 0.062 mm in length ($N = 7$) and 0.90 ± 0.035 mm in width ($N = 7$).

Predefecating Larva

No predefecating larvae of *A. carlini* were found, since none of the larvae excavated had completely consumed all of its provisions.

Inquilines and Parasites

Although *A. carlini* were not observed closely enough to note behavioral interaction between female bees and anthomyiid flies, two anthomyiid fly larvae were found in one *carlini* brood cell on 11 June 1976. One larva was slightly larger than the other (6 mm

as opposed to 5 mm) and both were covered by the liquid pollen mass at the bottom of the cell. A small, second instar, bee larva was found in this cell as well.

An unidentified species of *Nomada* was noted hovering around the sterile burrows of *A. carlini* in Brownfield Woods in April of 1976. On one occasion a *Nomada* female entered one of the woodland burrows for a few seconds. No *Nomada* were observed at the burrows of *A. carlini* in Mohannes field, New Brunswick.

DISCUSSION AND COMPARISON

Range

The range of *A. regularis* seems to be restricted to the Boreal or nearby Transition Zone, whereas that of *A. carlini* extends much further south in the Appalachians and even into the tall grass prairie regions. Although *regularis* and *carlini* are both clearly polylectic in flower preferences, *carlini* is far more so than *regularis* (Bouseman & LaBerge unpublished). It may be that the ability to use more pollen sources allows *carlini* to extend its range far beyond that of *regularis* which seems to be somewhat tied to ericaceous plants of the boreal regions. Furthermore, the nesting habits of *carlini* (nonaggregative in hard-packed soil), together with its ability to use many sources of pollen, may have allowed it to extend its range in relatively recent times due to the changes in environment by the action of civilization.

Nest Sites

In both localities (New Brunswick and Illinois) *A. carlini* seemed to be nongregarious, whereas *A. regularis* seemed to be a gregarious-nesting bee. It is not clear why some *Andrena* nest in aggregations while others are solitary. Perkins (1919) stated that some *Andrena* (notably *trimmerana, nitida* and *albicans*) never formed nesting colonies, while others *(A. cineraria)* will form dense colonies at one locality and at other localities will be scattered singly or in groups of two or three. Hirashima (1962) reported that burrows of *A. knuthi* were densely distributed in vegetated areas and sparsely distributed in bare ground. Nest scattering may be due to the fact that an entire area is suitable for nesting and aggregation due to the localized state of suitable sites. Although *carlini* is here considered to be more or less solitary, the roadbed site of Mohannes field did restrict the nests of *carlini* in a more or less linear series, although the nests were not closely aggregated. Nest scattering may also be the result of intense predation and/or parasite pressure. Presumably the more scattered the nests, the less likely they will all be located by parasites.

Osgood (1972) delineated characteristics common to areas within blueberry fields having good populations of nesting bees. The majority of nesting occurred at the highest point in a field or on a southwest slope. Plant cover was intermediate to sparse and the surface had good surface flow and drainage. Soil analyses indicated that wild bees nested in the greatest number where the O_2 horizon was loose and pliable with low organic carbon content. These characteristics generally fit the nesting site of *A. regularis* in Mohannes field, but not that of *A. carlini.*

Interspecific competition may account for the fact that nest sites of *carlini* and *regularis* were distinctly separated in Mohannes blueberry field. Since these are two closely related species (both in the subgenus *Melandrena*), using the same available pollen sources (notably cherry, apple and blueberry pollen), some type of competitive exclusion can be expected. Linsley *et al.* (1955) reported that under favorable conditions (an abundant pollen source, good weather conditions) three species of *Andrena* of the subgenus *Onagrandrena (mojavensis, oenotherae* and *deserticola)* shared the same available resources by differential nest site selection as well as slight differences in daily and diurnal pattern of activity. It is plausible that *regularis* and *carlini* co-exist in the same manner.

A final factor influencing nest site location in New Brunswick, not common to most species of *Andrena,* is burning; the common blueberry field management procedure practiced in early spring (strip-burning, rather than burning of entire fields). Burning serves a threefold purpose: it prunes and renews the blueberry plants, thereby increasing the yield and quality of fruit in the following year; it checks certain types of fungus diseases and pests that attack the plants (Phipps 1930); and it halts the encroachment of the surrounding forest (Kevan, unpublished). Furthermore, Boulanger *et al.* (1967) reported that this practice resulted in an increase in the number of native bees. Boulanger *et al.* (1967) were under the impression that *A. regularis* preferred the vegetative cover of unburned portions of the field. The present study shows that *regularis* may nest actively in burned portions of blueberry fields. Slope and drainage or soil characteristics may be more important than burning and the relative importance of these various factors on nest site selection is unclear.

In contrast, *A. carlini* seems to be a species which nests in sites devoid of both burned and unburned vegetation and the overall effect of burning in blueberry fields is probably minimal. The burrows of *carlini* found scattered in the leaf litter of Brownfield Woods near Urbana, Illinois, do not appear to be true nests but are probably refugia constructed by newly emerged females before nesting. Why some of these burrows seem to be occupied for as much as 30 days or more is unexplained. However, no marking studies have yet been done to show that a burrow is occupied by only one female and not by two or more in consecutive order.

Emergence and Mating

Boulanger *et al.* (1967) reported that native blueberry pollinators, especially the larger species of *Andrena,* made their appearance shortly before the blueberry blossoms. This is supported by observations made in Mohannes field in 1977; females and males of both species were observed on 12 May, 5 days before blossoms were found on blueberry plants. Furthermore, both *A. carlini* and *A. regularis* used other sources of pollen to initiate nesting before blueberries were in peak bloom.

Peak emergence dates for *A. regularis* in Mohannes blueberry field were 12 May for males and 18 May for females; strong evidence for proterandry (Boulanger *et al.* 1967). Peak emergence dates are not available for *A. carlini,* but collection records (Bouseman & LaBerge unpublished) indicate that males of both *carlini* and *regularis* emerge prior to the females. This is consistent with observations of *carlini* recorded in Brownfield and Busey Woods in Urbana, Illinois.

Copulatory behavior was observed for *A. carlini* in Illinois but has not yet been observed for *A. regularis.* Mating behavior is similar in the two species, occurring on flowers where both males and females are foraging shortly after emergence and where males are patrolling actively, probably seeking females.

Data regarding male longevity is meager, but evidence suggests that males of both *A. carlini* and *A. regularis* patrol vegetation for a week or more following emergence. Copulatory activity was recorded in Illinois for *carlini* as early as 2 April and as late as 15 April, allowing at least 13 days for patrolling behavior of males. In New Brunswick, *regularis* males had their peak emergence 12 May and were seen until 20 May, allowing at least 8 days or more for activity. Stephen (1966*a*) reported that males of *A. viburnella* patrolled the nesting site for 10–12 days following emergence. Michener & Retttenmeyer (1956) reported that males of *A. erythronii* marked between 9 and 16 March were still seen as late as 25 March.

Both *A. carlini* and *A. regularis* in Mohannes field presumably mate soon after emergence. All females captured and dissected from 12 May to 27 May had sperm in their spermathecae and the only female taken that did not have sperm was collected in a wire cone placed over an unopened nest of the previous season. Females of both species spend some time visiting flowers of rosaceous plants and blueberries in Mohannes field prior to nesting. Presumably this is the period of ovary maturation and pollen feeding is probably necessary for this to occur. The females of both *carlini* and *regularis* can be found in blind burrows in Mohannes field prior to 20 May. It is not clear whether these burrows become nests after ovary maturation is complete or whether new burrows are dug. In Brownfield Woods, Urbana, Illinois, blind burrows of *carlini* early in the season do not become nests later in the season, so far as we have been able to determine. The bees in Brownfield Woods presumably use the flowers of the forest floor for early foraging before nesting begins, and the burrows dug in the woods are assumed to be temporary refugia for these bees.

Nest Architecture

Nest structure is essentially identical in *A. carlini* and *A. regularis,* although nest site differed somewhat. Cells of both are coated with a highly polished, consolidated, internal surface characteristic of all *Andrena* species thus far studied. Thorp (1969) reported that the internal cell coat in *A. chalybaea* consisted of waterproof material. Rozen (1968) reported the same for *Meliturgula briensi* Friese (Andrenidae: Panurginae). Davis & LaBerge (1975) reported the shiny inside coating of cells to be waterproof in *A. erigeniae.* It is probably waterproofing in both *carlini* and *regularis* as well, but the nature of the substance impregnating the soil to form this layer remains undetermined.

Observations indicated that *A. carlini* burrows average slightly deeper than *A. regularis* burrows, and that *carlini* produces slightly more cells per burrow than does *regularis* on an average. The form of the burrows and the shape and size of the cells of the two species are very similar. New cells in both *carlini* and *regularis* are always found at the end of the main burrow shaft. A portion of the burrow next to a newly completed cell is filled with earth and the main burrow shaft extended in a slightly different direction and usually to a deeper level. Thus, no true laterals to the cells exist, but the so-called laterals (now filled with earth) to the completed cells are really parts of the main burrow shaft of the nest at an earlier stage of construction. This type of construction must represent only a slight evolutionary advance from those bees which construct a simple burrow with a single cell at the bottom. Likewise this seems to be a more primitive construction method than that of those bees which dig a deep burrow and then dig laterals, either regressively or progressively, to cells but retain the original deep burrow without a cell. Digging behavior of *A. carlini* was not observed, but was presumably the same as for *A. regularis* in Mohannes and essentially the same as that described for other *Andrena.* Davis & LaBerge (1975) and Michener & Rettenmeyer (1956) describe similar sequences of behavior for *A. erigeniae* and *A. erythronii,* respectively.

Nest-plugging behavior has also commonly been observed in *Andrena.* Davis & LaBerge (1975) observed *A. erigeniae* bringing soil up and plugging the nest about a centimeter from the surface and postulated that the bees were digging cells or a new burrow shaft. Linsley & MacSwain (1958) observed the same

behavior in *A. complexa* and *A. suavis* and Thorp (1969) observed similar behavior for *A. chalybaea*. Although plugging of all burrows in the nest aggregation never occurred, plugging seemed to occur only at the end of a series of foraging trips in *A. regularis*. This seems to indicate that the plugging of the main burrow was associated with digging of a new cell or burrow shaft.

Nest Recognition and Defense

Both *A. carlini* and *A. regularis* females seemed able to locate their nests and enter quickly, especially several days after nesting had begun. Earlier in the nesting season, disorientation was observed with females spending a few minutes to several minutes in finding their nests. Such variations in locating nests have been reported for several *Andrena*. Some disorientation may have been caused by the observer when excavating nests, and by the disruption of activity by parasites and predators. Early season disorientation is more common and females seemed to need to perform an orientation flight more often. Usually only one orientation flight per day was needed, and that was early in the day when the female first left her nest.

Davis & LaBerge (1975) state that nest recognition is due to both visual and olfactory clues. Recent advances have been made in determining the nature of compounds that have odoriferous qualities in *Andrena*. Bergstrom & Tengo (1974) reported that the Dufour's gland was relatively large in the genus *Andrena* and reached maximum size during nest construction. Furthermore, they reported that the gland seems to have two functions—it acts as an adhesive for nest galleries and as an odoriferous agent. Secretions from six species of *Andrena* were chemically analyzed *(bicolor, denticulata, nigroaenea, carbonaria, helvola* and *haemorrhoa)* and the main volatile components were identified as fornesyl and geranyl esters.

Behavioral observations of bees also indicate that nest marking occurs. Bergstrom & Tengo (1974) mentioned that *Andrena ovina* pressed its abdomen towards the entrance of the nest prior to departure. An anthophorid bee, *Eucera longicornis,* similarly pressed its abdomen against entrance walls, especially when the nest had been invaded by ants. Abdomen pressing was not observed in *A. regularis* or *A. carlini,* but marking of nests remains as a plausible explanation for burrow locating.

The aggregating behavior of *A. regularis,* as well as other species of *Andrena,* can also be understood in terms of olfactory stimuli. Bergstrom & Tengo (1974) reported that males and females of *A. flavipes* remained in nest areas due to odor characteristics of the nest site. Davis & LaBerge (1975) suggested that early emergers may attract later emergers by odor characteristics of newly excavated nest burrows. The tendency for some bees, such as *A. regularis,* to aggregate probably is of selective advantage, assuming that the early emergers choose the most suitable nest sites in a field and that the nest odor characteristics are important in locating the aggregation by incoming foraging bees. However, parasite pressure must override such advantages at times and dispersal must take place either after a site reaches saturation or before.

Defense of the nest by *A. regularis* was observed to be rather passive. Michener & Rettenmeyer (1956) observed that *A. erythronii* was not aggressive toward other bees, and Davis & LaBerge (1975) noted that *A. erigeniae* retreated when the entrance of its nest was invaded by a nabid bug. Avoidance tactics seemed to be used by *Andrena* females, rather than active defense of their nests.

Foraging and Provisioning

Both *A. regularis* and *A. carlini* are polylectic bees, a common adaptation of early spring bees. Sampling of pollen from females and from pollen in cells of both species indicated that pollen from *Prunus pennsylvanicus, P. virginiana, Aronia arbutifolia, Crataegus* sp., *Amelanchier* sp., *Malus* sp., and *Fragaria* sp., were all used at least to initiate nesting. Later, as blueberry plants came into bloom, most or all of the pollen brought into the nest was blueberry pollen.

The molded provisions of *A. carlini* and *A. regularis* are indistinguishable. Stephen (1966*a*) described a pollen mass for *A. viburnella* that was similar to that of *carlini* and *regularis* in that it was not a spherical ball but was craterlike. The *viburnella* pollen mass seems to be more deeply craterlike than that of either *regularis* or *carlini.* It was noted that the consistency of the pollen in cells of the same burrow, especially during larval development, varied from a soupy mass to a dry, cakey mass. Whether this was a change in the pollen mass after the larvae began feeding or occurred before the egg was laid, was not determined. Cells with eggs all had cakey, dry pollen masses and some of the cells with larvae did not have a semiliquid mass but remained cakey.

Foraging activity for both *A. carlini* and *A. regularis* in Mohannes field was continuous from early in the morning until sunset. Females did not usually begin foraging until the temperature reached about 13°C, and days in which the temperature dropped suddenly found more females returning to the nests early than on other days. Inclement weather stopped foraging activities, although both species did bring pollen into their nests on mild, light rainy days. As mentioned above, foraging was also interrupted by digging activities of the females.

Foraging trips for *A. regularis* ranged from 23 to 272 minutes. No such information was recorded for *A. carlini,* but it seems likely that the time spent foraging is similar to that of *regularis.* Foraging time

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