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The Nesting Habits and Immature Stages of Andrena (Thysandrena) candida Smith (Hymenoptera, Apoidea)

Nabil N. Youssef

George E. Bohart
Utah State University

THE NESTING HABITS AND IMMATURE STAGES OF *ANDRENA* (*THYSANDRENA*) *CANDIDA* SMITH (Hymenoptera, Apoidea)[1]

NABIL N. YOUSSEF[2] AND GEORGE E. BOHART[3]

ABSTRACT

Andrena candida Smith is a spring and early summer, double-brooded, species from the western United States. It has a wide host range and a pronounced mock-orangelike odor emanates from its head. Nesting occurs in small aggregations in flat, hard-packed, partially exposed ground. The average nest had main burrows about 10 cm long and 3 laterals, each about 1 cm long and ending in a single, slightly inclined cell. Completed nests were plugged with soil. Each cell was provisioned with a slightly flattened sphere. The egg was arched, with the anterior end directed toward the cell cap. The average life cycle was as follows: egg, 4 days; feeding stage, 8 days; defecation, 3 days; postdefecation (prepupa), 16 days; pupa, 11 days. Fecal material was deposited in a flattened scale of shingled layers in the lower, terminal portion of the cell.

Morphological differences between the first and last stage larvae are described and illustrated. The general body form of bee larvae is emphasized as an important, but often neglected, character.

LITERATURE REVIEW

Biological information is available for only a small fraction of the enormous number of species of *Andrena*. Malyshev (1926) published on 11 Russian species. Friese published some short papers on the an extensive paper that included information (some of it quite detailed) nesting habits of *Andrena* in northern Europe (1882, 1921) and some longer ones on bee biology that included notes on several additional species (1891, 1923). Hirashima (1962) gave relatively detailed accounts of the biology of four Japanese species. A few North American papers contain brief descriptions of nesting habits (MacSwain, 1945; Sivik, 1954; Linsley *et al.*, 1955, 1963; Linsley and MacSwain, 1956, 1959). The papers by Linsley *et al.* and Linsley and MacSwain include much data on the flower-visiting habits of species specializing on Onagraceae and *Ranunculus*. Stephen (1966a) wrote a more complete paper on the nesting habits of one species (*A. viburnella*). Michener and Rettenmeyer (1956) made the most complete study published for any species of *Andrena*, *A. erythronii*, in which they compared the biological features of this species with those described in the literature for many other *Andrena*. In the same paper they published original observations on *Andrena miserabilis* (as *bipunctata*). The only detailed descriptions of the immature stages of *Andrena* are those given by Michener (1953) for the mandibles and spiracles of *A. complexa* and

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[1] In cooperation with Utah Agricultural Experiment Station. Accepted for publication February 1, 1968.

[2] Research Associate, Department of Zoology, Utah State University, Logan, Utah.

[3] Entomology Research Division, Agr. Res. Serv. U.S.D.A., Logan, Utah.

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A. erythronii and those of Stephen (1966b) for *A. viburnella*. The only biological note we could find concerning the subgenus *Thysandrena* is that of Linsley (1937) on the occurrence of double broods in *A. candida*.

In the subsequent discussion, the literature citations for statements concerning species other than *A. candida* can be found by referring to the following tabulation:

LIST OF *ANDRENA* SPECIES CITED AND NAME OF INVESTIGATOR

A. (*Andrena*) *armata* Gmelin	Pickles 1940
A. (*Plastandrena*) *astragaline* Hirashima	Hirashima 1962
A. (*Plastandrena*) *bimaculata* (Kirby)	Malyshev (1926)
A. (*Thysandrena*) *bisalicis* Viereck	Yager and Rozen (1966)
A. (*Thysandrena*) *candida* Smith	Present paper
A. (*Melandrena*) *cineraria* (Linn.)	Malyshev (1926)
A. (*Geandrena*) *complexa* (Viereck)	Linsley and MacSwain (1959)
A. (*Tylandrena*) *erythrogaster erythrogaster* (Ashmead)	Rau (1935)
A. (*Tylandrena*) *erythrogaster subaustralis* Ckll.	Bohart (1952)
A. (*Leucandrena*) *erythronii* Robertson	Michener and Rettenmeyer (1956)
A. (*Melandrena*) *heterura* Cockerell	Unpublished (Bohart and Youssef)
A. (*Chrysandrena*) *knuthi* Alfgen	Hirashima (1962)
A. (*Gymnandrena?*) *macra* Mitchell	Sivik (1954)
A. (*Larandrena*) *miserabilis* Cresson	Unpublished (Bohart); Michener and Rettenmeyer (1956) (as *bipunctata* Cresson)
A. (*Onagandrena*) *oenotherae* Timberlake	Linsley and MacSwain (1956)
A. (*Melandrena*) *parathoracica* Hirashima	Hirashima (1962)
A. (*Melandrena*) *perplexa* Smith	Parker and Böving (1924)
A. (*Leucandrena*) *placida* Smith	Unpublished (Bohart)
A. (*Andrena*) *rhodotricha* Linsley	MacSwain (1945)
A. (*Onagandrena*) *rozeni* Linsley and MacSwain	Linsley, MacSwain, and Raven (1963)
A. (*Melandrena*) *vaga* Panzer	Malyshev (1926)

A. (Melandrena) viburnella Stephen (1966a, b)
Graenicher

DIAGNOSIS OF ADULT

A. candida is a moderately small (9 mm long), dark-colored species with distinct but generally rather weak, dark blue reflections (weakest on scutellum and clypeus). The body is minutely roughened throughout, and the punctures are mostly small and separated by several puncture diameters. There are distinct lateral white fasciae on terga II to IV. The pubescence is tan to white in the female except for dark brown anal fimbria and facial foveae. The male has a strong admixture of dark hair on the face and cheeks.

Both sexes are characterized by a strong mock-orangelike odor emanating from the head. We have found a few other species of *Andrena* with a similar but less pronounced fragrance.

DISTRIBUTION, SEASON, AND HOST RANGE

A. candida is widely distributed in the western United States. There are records of its occurrence in California (northern and southern), Oregon, Washington, Idaho, Utah, and Colorado. It inhabits coastal, agricultural valley, desert, and mountain environments and it is found at various elevations as high as 9,000 feet.

In common with many species of *Andrena, A. candida* is one of the first bees to appear in the spring. It flies for three weeks to one month and then reappears about one month later. Linsley (1937), quoting P. H. Timberlake, noted its apparently double-brooded condition, which he regarded as unusual (but not unique) in the genus.

In northern Utah, both sexes (with males predominating) appear in April on the earliest-blooming willows. Males generally disappear in early May, but females remain active until the second or third week of that month. Both sexes are found again in the second half of June or the first half of July, depending upon the season. Females were collected as late as the end of July in 1967, a year with unusually cool, wet weather during May and June.

Although the field collections clearly indicate two broods, we were unable to observe a second brood in the small nesting site studied in 1967. Perhaps the second brood is only partial, and the site we observed was too small for a significant number of second generation bees to appear. Our records on the development of immature stages in the laboratory support the timing of the broods observed in the field. Eggs laid on May 13 became adults on June 23 (Fig. 1). Probably the second brood overwinters in the adult stage since this is usually the case in species appearing early in the year.

The two broods differ somewhat in color. Linsley mentioned the paler facial pubescence of the males in the second brood. We have noted that in both sexes the bluish reflections of the second brood are

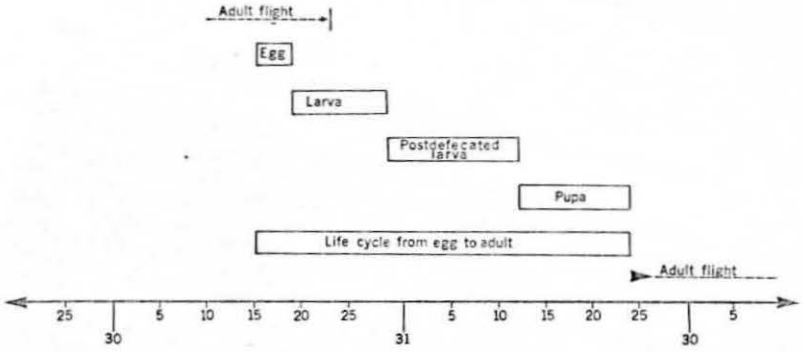


FIG. 1. Diagram of average life cycle of *Andrena candida*.

less pronounced. Also, there is a tendency for second brood females to have less roughening on the scutum, thus making the punctures more prominent.

A. candida has a wide host range. In northern Utah, it visits *Salix discolor* Muhl., which is the first plant to bloom in the spring, even before the catkins open. When this willow is fading, the principal host plants become the umbellifers *Lomatium grayi* Coult. & Rose and *Cymopterus longipes*, S. Wats. While these plants are still in bloom, the foraging emphasis shifts back to trees (*Salix* spp., *Acer grandidentatum* Nutt., *Acer platanoides* L., *Malus pumila* Mill. and *Amelanchier* spp.). There is less data available on host plants for the second brood, but late collection records include *Conium maculatum* L., *Daucus carota* L., *Melilotus alba* Desr., *Medicago sativa* L., *Sisymbrium officinale* (L.), *Brassica nigra* (L.), and *Salix exigua* Nutt. Host plant genera recorded for the species in California by Linsley (1937) include *Salix, Cryptantha, Eriogonum, Rhamnus, Ceanothus, Brassica, Sisymbrium, Eriodictyon,* and *Nemophila.*

NESTING SITES

The nesting site we studied was about two miles east of Mendon, Cache County, Utah (elevation 5,200 feet), along a dirt road that passed through a sloping meadow near a wooded area populated principally by *Acer grandidentatum*. Most of the nests were scattered along the hump of the road between the tire tracks over a distance of about 45 meters. In the most concentrated zones the nests averaged about five per square meter, but on most of the site the nests were probably fewer than one per square meter. A few nests were also found along the side slopes of the depressions of the tire track. At the time of nesting, the road hump was covered with small seedlings, some of which (a *Phlox* and a blue-flowering *Nemophila*) were already in bloom, though only an inch or two high. The nest mounds were often difficult

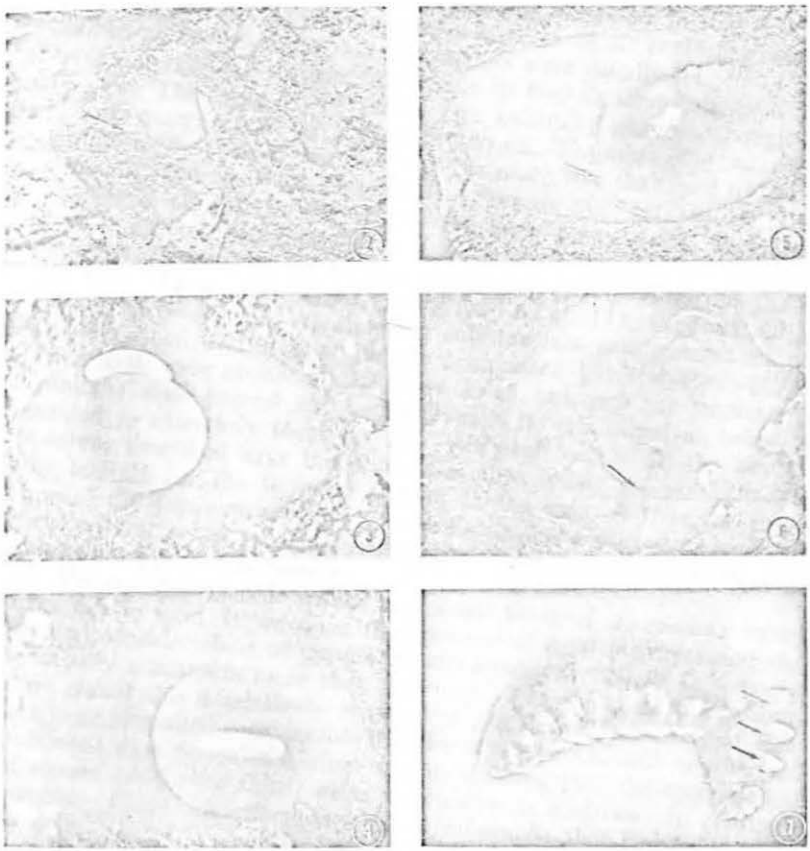
to see because they were placed next to the largest seedlings. The soil was a well packed dark-colored mountain loam with many small, angular pebbles. The sod was moist and rather easy to excavate during the nesting season, but it became hard and dry (powdery on top) in July. Apparently, many species of *Andrena* nest in hard-packed, relatively unshaded surfaces of roadways or paths (*A. erythronii, A. erythrogaster, A. miserabilis,* and *A. placida*). Other examples of *Andrena* nests in open situations include those in flat, sandy stream banks or washes (*A. erythrogaster, A. oenotherae*) or in open ground, but in the depressions and bottoms of shaded road cuts (*A. rozeni*). Probably most species of *Andrena* prefer well vegetated sites close to grass clumps or near the crowns of large plants (*A. knuthi, A. parathoracica, A. hetcrura*), but nests of these species are more difficult to locate. A similar nesting situation is that afforded by lawn grass, often chosen by *A. viburnella* and *A. perplexa. A. complexa* also nests in hidden sites, choosing wooded areas and hiding its tumuli under leaves, bark strips, and other objects. Several species nest in both flat ground and in nearby low vertical banks (*A. parathoracica* and *A. astragalina*). At least one species (*A. rhodotricha*) nests in high vertical banks between the exposed roots of overhanging trees.

NEST BURROWS

A. candida excavated its nest by using the same procedures followed by *A. macra* and *A. erythronii*. When soil was pushed out of the burrow by the tip of the abdomen and allowed to fall naturally from the accumulating pile, the tumulus (at least, as first formed) was always symmetrical with a central entrance not depressed in a crater. Tumuli of *A. candida* averaged 40 mm wide and 15 mm high. When a tumulus was blown or brushed away, there remained a steeply conical turret about half as high and one-third as wide at the base as the tumulus. This cone was composed of moist, hard-packed soil (Fig. 2). Malyshev reported a similar cone in the tumulus of *A. vaga,* but Stephen and Michener and Rettenmeyer did not find such a structure in tumuli of *A. viburnella* or *A. erythronii.*

The nest entrance of *A. candida* had the same diameter as the main burrow (3.6 mm). The main burrow extended downward in a vertical or near-vertical direction for 3 to 8 cm and then angled sharply to about 45° from vertical (Fig. 8). In extreme cases, this second segment of the main burrow was nearly horizontal (Fig. 9). It varied in length from 3 to 5 cm.

An L-shaped main burrow was also described for *A. oenotherae* and *A. rozeni* though these species have much longer burrows. The main burrows of the Japanese species described by Hirashima were somewhat similar but more irregular and they lacked well defined vertical and horizontal sections. Michener and Rettenmeyer illustrated a main burrow of *Andrena erythronii* that was almost entirely vertical and had several laterals diverging from its lower end.



FIGS. 2–7. *Andrena candida*. FIG. 2, Nest entrance surrounded by conical turret of cemented particles. FIG. 3, Cell with pollen ball and egg in lateral view. FIG. 4, Cell with pollen ball and egg in dorsal view. FIG. 5, Cell with third or early fourth stage larva. Note liquid surrounding pollen ball. FIG. 6, Artificial cell with fourth stage larva. Note "posterior pseudopod" used for rotating ball. FIG. 7, Postdefecated larva. Note thoracic tubercles.

In most *A. candida* nests studied, the laterals (½ to 1 cm long) fanned out from near the end of the main burrow (at a depth of about 9 cm), but in one nest with an unusually long first segment, the uppermost lateral diverged near the beginning of the second segment (Fig. 8); the other laterals in this nest were unusually deep (about 12 cm). The laterals were slightly narrower than the main tunnel and each narrowed to a neck (2.9 mm) leading to a single cell oriented in the same (or nearly the same) direction as the lateral itself. Occasionally the narrow neck area extended all the way from the cell to the main

burrow. This pattern of laterals and cells is similar to that described for *A. complexa*. The arrangement in nests of *A. erythronii* was described as being similar, but the laterals were usually longer. *A. cineraria* was reported to sometimes make its laterals longer than the main burrow. The nests of *A. candida* are unusually shallow, though only slightly more so than those of *A. erythronii*. The nests of *A. miserabilis* are often 35 cm deep though the soil is much like that used by *A. candida*. In sandy soil, the nests of *A. rozeni* are over 100 cm deep.

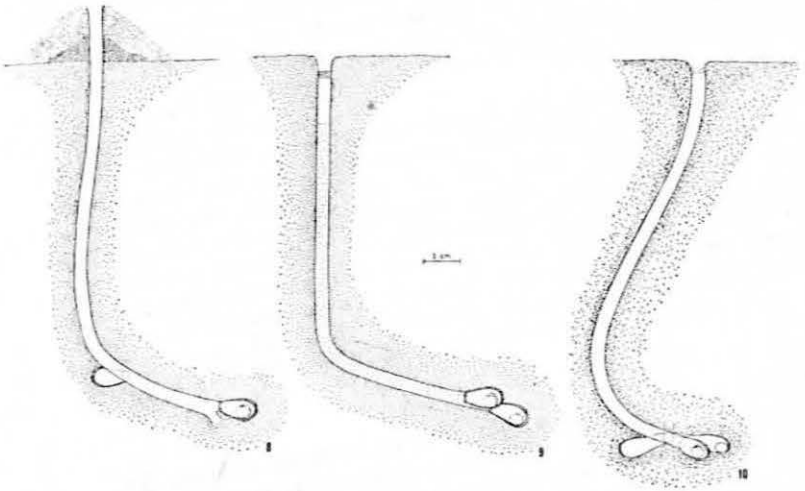
Nearly all descriptions of *Andrena* nests indicate that each lateral ends in a single cell rather than a linear chain of cells, but Hirashima found chains of cells for all four species he studied. According to him (p. 13), "They were placed end by end (Fig. 13), as usual for the species of *Andrena*." A somewhat intermediate arrangement of cells was described and figured for *A. bimaculata* by Malyshev (1926). These cells were apparently in linear series, but each one angled away from the main burrow and could perhaps be considered as being appended to extremely short laterals. Although nearly all the nests of *Andrena* described have the cells oriented in nearly the same plane as the laterals (or the terminal portion of the main burrow, as in the case of the Japanese species), *A. viburnella* was reported to have vertical cells attached to short, nearly horizontal laterals arranged along a nearly vertical main burrow.

The number of cells in the completed nests of *A. candida* varied from two to four. Based upon the presence of eight ovarioles and theoretical considerations of population dynamics, we believe this species habitually constructs more than one nest. The shortness of the burrows makes this a relatively economical practice. Michener and Rettenmeyer presented considerable data for *A. erythronii* and summarized published data for several other species showing that the construction of second (and even third) nests is common in *Andrena*. In contrast, Stephen (1966a) described nests of *A. viburnella* that had from 12 to 18 cells.

All the nests we excavated had short soil plugs a few millimeters below the entrance, often blocking the internal chimney of the tumulus. The incomplete nests were otherwise clear of soil in the main burrow except for one that had a loose mass near the middle of the burrow. This mass was probably soil taken from a recently excavated (unpolished) cell. *A. erythronii* was described as having the main burrow loosely filled with soil, even while it was provisioning the cells.

In the nests of *A. candida* (and probably in those of all other species), each lateral was completely plugged with soil soon after the cell was capped. The plug was composed of small lumps of soil indistinguishable in profile from those used in the cell cap.

After the nests were completed, the main burrow was filled with moderately well packed soil, except for a centimeter or two below a short entrance plug. The empty space may be the result of soil settling below the more firmly packed entrance plug. A similar space was



FIGS. 8–10. Diagrams of nests (longitudinal sections) of *Andrena candida*.

shown in one of the nests of *A. erythronii* figured by Michener and Rettenmeyer.

CELLS

The brood cells ranged from horizontal to about 20° from horizontal (Fig. 10). In one nest, they were nearly parallel to each other (Fig. 9), but usually they diverged rather sharply (Fig. 10). Because the laterals were short and began close to one another, the cells were often less than a cell width from their nearest neighbor and were never more than 20 cm from the most distant cell in the nest. The shallowest cell found was 10 cm from the surface, and the deepest was 14 cm. Although horizontal or nearly horizontal cells are the rule for most nests of *Andrena* described [in spite of Bischoff's statement to the contrary (1927)], vertical or nearly vertical cells were reported for *A. cineraria* and *A. viburnella*.

The cells were first excavated to form a roughly urn-shaped chamber and then lined with firmly packed soil and smoothed to form the final cell cavity. The particles of earth lining in *Andrena* cells, according to Pickles and Michener and Rettenmeyer, are cemented by a glandular secretion. Stephen (1966a) apparently considered that *A. viburnella* excavated its cell to the final shape and then impregnated the wall with a liquid material. The lining of the cells of *A. candida* varied in thickness from 1 mm at the terminal portion of the cell to ½ mm near the neck. The lining was fragile and could not be pulled away from the surrounding soil, except in small fragments.

The inner surface of the completed cell was given an extremely thin lining with a transparent, waxy-appearing substance extending

basally into the neck slightly beyond the cell cap. According to Stephen (1966a), the clear lining of the cells of *A. viburnella* covers only the terminal two-fifths of the cell and is notably thicker at the terminal end. However, cells of this species that we have seen had the lining complete but somewhat thinner toward the cell neck. According to Malyshev (1926), the lining material of *Andrena* cells is insoluble in cold water, chloroform, and ether but breaks up in boiling water. We confirmed these statements but found that the lining also dissolves in methylene chloride.

The completed cells were urn-shaped, with the inside length varying from 9 to 10 mm and the maximum width from 5.0 to 5.3 mm. Width at the cap was 3.0 mm (Fig. 3). The inner wall of the cell, though smooth, had a somewhat irregular profile, especially toward the cap. The cell cap was formed of small particles of soil constructed as a continuous spiral starting from the neck wall. The cap was nearly flat but slightly invaginated toward the plug. Caps of this type are common to most *Andrena,* but in *A. erythronii,* the spiral construction is not visable, and in *A. viburnella,* the invagination is quite deep.

PROVISIONS

A. candida provided its cells with a moist but firm ball of pollen in the shape of a flattened sphere (the equatorial axis being greater than the polar); in addition, the upper side was somewhat flatter than the lower (Fig. 3). The three balls measured showed a variation in total size and polar to equatorial ratio as follows: 4.1:4 mm; 4:3.8 mm; 3:2.9 mm. The first pollen load brought to the cell was molded as a rough, moistened sphere. Subsequent loads were added as concentric layers, and the final load was given some extra moisture and more carefully shaped and smoothed. The pollen ball of *A. erythronii* resembled closely that of *A. candida.* Those described for *A. knuthi* were similar but more nearly spherical. Pollen balls of many species, including *A. candida,* have no liquid in the cell until the larva starts feeding, but the pollen masses of several species were reported to be surrounded by liquid (*A. parathoracica* and *A. perplexa*).

IMMATURE STAGES

The glistening white egg was elongate, curved, circular in cross section, and smaller anteriorly than posteriorly. It was 1.8 mm long by 0.4 mm wide at the middle (Figs. 3, 4).

The egg was laid on top of the pollen ball with the anterior end toward the cell cap. Both ends touched the ball, but the middle portion was free. As the embryo developed, the curvature decreased until it paralleled the surface of the ball (Fig. 3 shows an intermediate stage). Although this placement of the egg seems to be the rule for most *Andrena,* the eggs of *A. vaga, A. cineraria,* and *A. viburnella* are placed in a semi-erect position. Stephen described in detail a "crater" on the

top of the pollen mass of *A. viburnella* in which the egg was inserted to a depth of 1 to 1.5 mm.

The larva of *A. candida* fed by swinging its head from side to side and scraping pollen from the ball with its mandibles. Periodically, it raised its head and made chewing motions. In the first larval stage, only a few pollen grains were held between the mandibles, but later a larger mass was handled at one time. By this method of feeding, the larva first made a small notch in the ball. As the larva grew, the notch became longer, wider, and deeper and progressed forward and down the anterior face of the ball (Fig. 5). Simultaneously the posterior end of the larva grew down and around the posterior face of the ball until eventually the head and anal segment almost met. At this time, the ball was picked up and held in the larva's ventral curvature until it was consumed (Fig. 6). This description compares rather closely with that of *A. erythronii*.

In the laboratory 12 larvae were raised from the egg stage at 25–27° C on pollen (trapped from colonies of *Apis mellifera* L.) mixed with enough 25% sugar solution to approximate the texture of the natural ball. The rearing was carried out under sterilized conditions. The average life cycle is shown in Fig. 1. It was not possible to distinguish the different larval instars because of the need to maintain sterile conditions.

Defecation started one day after feeding was completed. The fecal material, as seen in the field, was deposited in a flattened scale at the lower, terminal portion of the cell, and elongated and flattened fecal pellets were fused together in several shingled layers.

Pigmentation of the pupa progressed somewhat differently from that of other bees. The head and thorax darkened first, and then pigmentation progressed from the posterior to the anterior end of the abdomen.

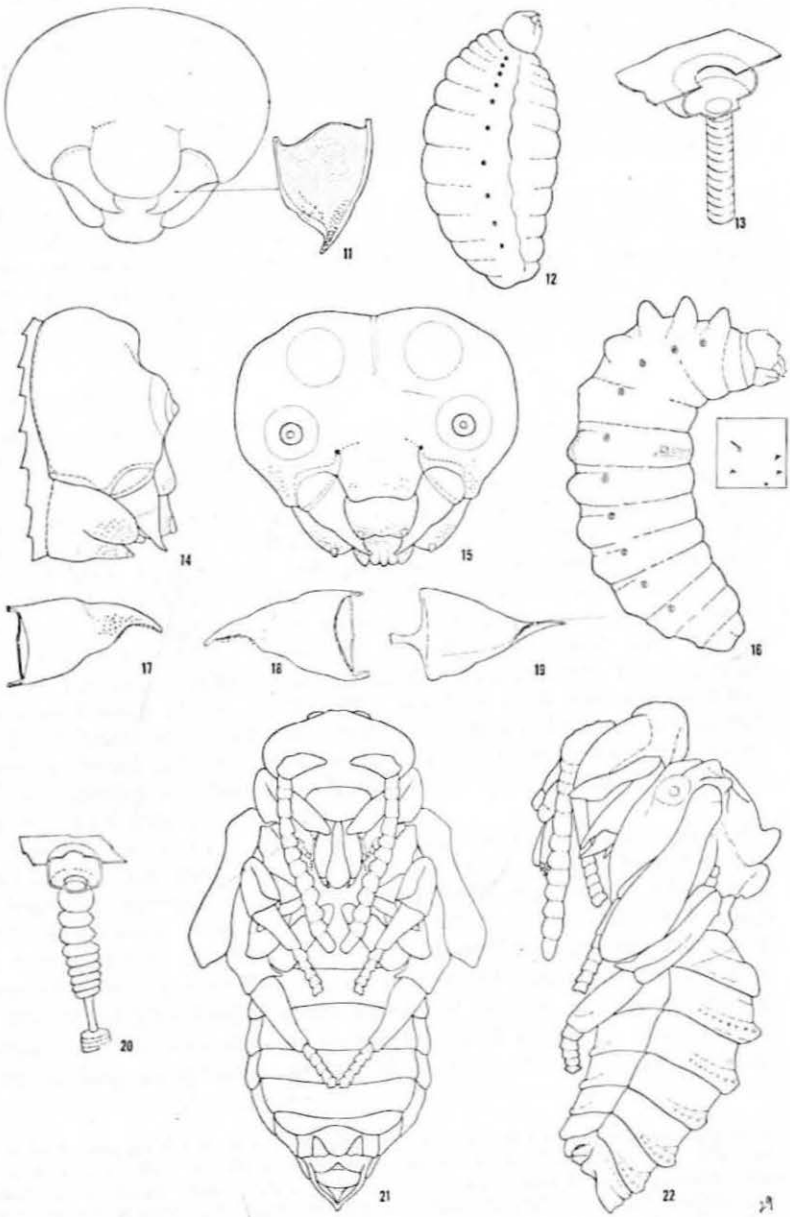
EXTERNAL MORPHOLOGY OF IMMATURE STAGES

Although the mature larvae of several species of *Andrena* have been described, the following description is apparently the first for a larva of the subgenus *Thysandrena*. Yager and Rozen (1966) described the pupa of three species of *Andrena* and included a description and drawing of a pupal *A.* (*Thysandrena*) *bisalicis*. Also, Michener (1953) and Stephen (1966b) described and figured the external morphology of *Andrena* larvae in detail, but they confined themselves to the post-defecated larvae.

The 12 specimens of *A. candida* studied were larvae and pupae reared from eggs taken from cells in the field and placed on simulated pollen balls in the laboratory.

First stage larva

Head (Fig. 11): Frontovertical complex oval in profile; protuberances and antennal convexities lacking; antennal papillae indistinct;



FIGS. 11–22. *Andrena candida*. FIG. 11, Head and left mandible of first stage larva (note that mandible of second stage larva is encased in that of first). FIG. 12, First stage larva (lateral view). FIG. 13, Spiracle and associated structures of first

head with a few setae scattered mainly over mouth parts; tentorium present and complete; marginal epistomal ridges not prominent; cleavage line and parietal bands not evident; labrum gradually pointed and without tubercles; mandibles moderately sclerotized and bent apically, with two minute teeth on inner margin; maxillary palpi not evident; cardo not separated from stipes; labium recessed and without palpi; prementum not separated from postmentum; salivary opening not evident.

Body (Fig. 12): Slightly arched with mediodorsal hump; intersegmental furrows distinct, without annulations; dorsolateral tubercles absent; integument with setae dorsally and ventrally. Spiracles relatively large; atrium cylindrical, apparently lacking spines or ridges; not projecting above body integument; primary tracheal opening without collar; subatrium connected directly to tracheal trunk (Fig. 13).

Postdefecated larva

Head (Figs. 14, 15): Frontovertical complex rounded, sclerotized, and with a pair of abrupt protuberances arising mediodorsally of antennal convexities; antennal convexities prominent, with distinct short, conical antennal papillae. Labrum, maxillae, labium, genal areas with many setae; marginal thickening moderately developed, but posterior tentorial pits, hypostomal and pleurostomal thickenings more pronounced; cleavage line weak; parietal bands absent; epistomal suture indistinct; labroclypeal suture distinct; labrum truncate, with pair of large lateral tubercles; mandibles strongly sclerotized and sharply pointed, the inner apical margin serrated to base of cusp, the cusp with fine dorsal teeth (Figs. 17, 18, 19); maxillae with apex directed forward; cardo not separated from stipes; maxillary palpi large and apical, almost as broad as long; labium with palpi larger than maxillary palpi; salivary opening on small tubercle forming a "salivary lip"; prementum not separated from postmentum.

Body (Figs. 7, 16): About 8 mm long (measured along spiracular line) and 2.5 mm wide in lateral view; 7-shaped, sharply bent between postcephalic segments 3 and 4; postcephalic segments 1 through 3 with conspicuous, conical dorsolateral tubercles; segments 4 through 10 with rounded dorsal tubercles and dorsal annulations; each segment with narrow mid dorsal band and broad transverse ventral zone of minute spicules having broad bases and narrow, acuminate apices; integument otherwise smooth except for small group of setae (about twice as long as spicules) at lateral portions of transverse spiculate

←

stage larva (longitudinal section of spiracle). FIG. 14, Head of postdefecated larva (lateral view). FIG. 15, Head of postdefecated larva (frontal view). FIG. 16, Postdefecated larva (lateral view). FIGS. 17–19, Left mandible of postdefecated larva (dorsal, ventral, inner lateral). FIG. 20, Spiracle and associated structures of postdefecated larva (longitudinal section of spiracle). Note atrial collar and raised atrial chamber. FIG. 21, Pupa (ventral view). FIG. 22, Pupa (lateral view).

band and a few scattered setae in general area of spiracles. Spiracles with atrium produced above body integument; without inner spines or ridges; with slightly convex, almost flat preatrium; collar present; anal slit opening medially (Fig. 20).

Pupa (Figs. 21, 22)

Head densely covered with minute, dome-shaped spicules except on mandibles, maxilla, and labium; thorax ventrally and laterally covered with minute, triangular to flame-shaped spicules, especially around wing bases; femora, tibiae, basitarsi densely covered with minute thorn-shaped spicules; wings and coxae smooth. Abdomen with mid dorsal area covered with minute (mostly) sharply pointed spicules, the spiculate zone much broader at marginal folds and posterior halves of each segment; each tergum with a posterior submarginal row of dome-shaped "macro-spicules" (= tergal spicules of Michener, 1954).

Gross external morphology not differing significantly from that described by Yager and Rozen (1966) for *A.* (*Thysandrena*) *bisalicis*, except for absence of any propodeal protuberances.

Discussion

Although the first and last stage larvae of *A. candida* feed on the same type of food (a moist but firm mass of pollen), they differ morphologically in many features. The first stage lacks the dorsolateral tubercles that are so conspicuous on the postdefecated larva. The entire integument of the first stage is covered with setae, but in the postdefecated larva, setae are limited to the ventral side. In the first stage, the labrum, maxillae, and labium have no tubercles or palpi; these are distinct and large on the postdefecated larva. The mandible of the first stage is smooth on the outer margin and has only two teeth on the inner margin (Fig. 11); whereas the mandible of the second stage larva has three rows of teeth on the outer dorsal margin and five teeth on the base of the mandibular cusp. Also, in the postdefecated larva, the inner margin of the mandibular cusp is heavily serrated (Fig. 17). The spiracular atrium is larger in proportion to the insect than that of the postdefecated larva. Also, the subatrium is connected directly to the tracheal trunk rather than being separated by a constriction.

The postdefecated larva can be differentiated from other described species (belonging to at least three subgenera) of the genus *Andrena*. In *A. candida*, the labial palpi are larger than the maxillary palpi, but they are "minute" in the other four species studied. Michener (1953), in his description of the larvae of Andrenidae, page 1033, stated, "Thus the salivary opening is reduced to a curved slit with no lips." In *A. candida*, the salivary opening is located on a lobelike structure. Also, the atrium has no ridges or spines, but those of the other four species have ridges. The general body form of *A. candida* is more sharply bent than that of *A. viburnella*, and apparently it is also somewhat more slender. We have observed that the body form of postdefecated larvae

in bees is often quite characteristic, even at the species level. Probably, future descriptions of hymenopterous larvae should give greater emphasis to this aspect.

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