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Nesting Habits of Three Species of *Andrena* in Hokkaido (Hymenoptera, Apoidea)¹⁾

By

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(With 28 Text-figures and 1 Table)

Although it is principally limited to the Holarctic Region, the genus *Andrena* Fabricius is one of the largest bee genera both in species and individual numbers. Among about two thousand species so far described, only a limited number of species have hitherto been studied with respect to the bionomics.

Since Friese (1882) gave accounts on the nesting habits of *Andrena pratensis* Nylander (= *ovina* Klug), several papers, most of which are merely brief notes, have been published on the bionomics of the European and Nearctic species. The most detailed work is that by Michener and Rettenmeyer (1956) on a Nearctic species, *A. erythronii* Robertson, which will be cited in the subsequent pages. In a recent paper concerning *A. candida* Smith, Youssef and Bohart (1968) gave a list of previous information on the bionomics of various species. As to the Japanese species, the nesting habits are so far known only in six species, *A. (Chrysandrena) knuthi* Alfken, *A. (Gymnandrena) parathoracica* Hirashima, *A. (Plastandrena) astragalina* Hirashima, *A. japonica* (Smith), and *A. (Calomelissa) prostomias* Pérez (Hirashima 1962, Kawamura 1957, Okumura 1964).

Since 1965, the writer has engaged in the biological studies of this genus in Hokkaido through two approaches, these are, the biofaunistic studies by quantitative sampling on flowers and bionomic studies of particular species. The results along the first approach were partly given in Sakagami and Matsumura (1967) and Matsumura and Munakata (1969). The present paper deals with the results along the second approach and describes the nesting habits of three species, *A. (Micrandrena) sublevigata* Hirashima, *A. (Gymnandrena) watasei* Cockerell, and *A. (Cnemidandrena) seneciorum* Hirashima, among which the habits of *Micrandrena* and *Cnemidandrena* are so far unknown. For the sake of convenience, the outline of habits and some numerical data on nest structure are summarized in Table 1.

Before going further, the writer wishes to express his sincere thanks to Prof. M. Yamada and Dr. S. F. Sakagami, Zoological Institute, Hokkaido University, for their kind guidance to the present study.

1) Contribution No. 879 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

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Table 1. Synopsis of some biological characters in three andrenid species.
(* Showing minimum, average and maximum values)

Character	Species		
	<i>A. sublevigata</i>	<i>A. watasei</i>	<i>A. seneciorum</i>
Flight season in Hokkaido	Late April~mid. June	Late April~early July	Late July~mid. Sept.
Nest site observed	Flat ground, open to sparsely grassy	Flat ground, sparsely to densely grassy	Slightly inclined ground, sparsely grassy
Spatial distribution of nests	Forming aggregations		Discrete distribution ?
Nest type	Linear (allodalous)	Stationary branched (heterodalous)	
Diameter of entrance	2.0~3.0 mm	5.5~7.0 mm	4.5~5.5 mm
Diameter of burrow	2.5~3.5 mm	6.0~7.0 mm	5.0~6.0 mm
Depth of nest bottom*	5.5, 10.3, 13.5 cm	8.0, 15.3, 18.0 cm	11.0 cm
Depth to cell*	5.0, 9.7, 13.5 cm	8.0, 14.7, 17.0 cm	9.0, 10.0, 11.0 cm
Shape of cell	Elongate oval		
Orientation of cell	Horizontal to 40°	10° to 45°	Horizontal
Cell wall	With 2 layers, inner layer polished		
Cell size			
Diameter *	3.5, 4.1, 4.5 mm	7~8 mm	7.0~7.5 mm
Length *	7.0, 8.2, 9.0 mm	13~15 mm	14~15 mm
Number of cells per nest *	2, 3~4, 5	2, 3, 5,	3
Pollen ball			
Diameter *	2.6, 3.1, 3.5 mm	4.3~6.4 mm	—
Height *	2.4, 2.8, 3.3 mm	3.5~5.2 mm	—
Weight *	10, 14, 17 mg	—	—
Egg			
Diameter	0.3~0.5 mm	0.49~0.73 mm	—
Length	1.7~1.8 mm	2.56~2.68 mm	—
Hibernating stage	Adults within cells		(Prepupa ?)

***Andrena (Micrandrena) sublevigata* Hirashima**

A. sublevigata is a small shiny black species (body length: ♀ 6~7 mm, ♂ 5.5 mm). It is one of the dominant andrenid species in Sapporo, occupying the highest

rank in relative abundance during late April to middle May (Sakagami and Matsumura 1967), though not always common in some other areas in Hokkaido. This is one of the early occurring species in Sapporo, with the flight season from late April to June. The seasonal shift of flight activities of both sexes is given in Fig. 1 top, together with the relative age of each individual, all based upon the periodical sampling made in the Campus and Botanical Garden, Hokkaido Univer-

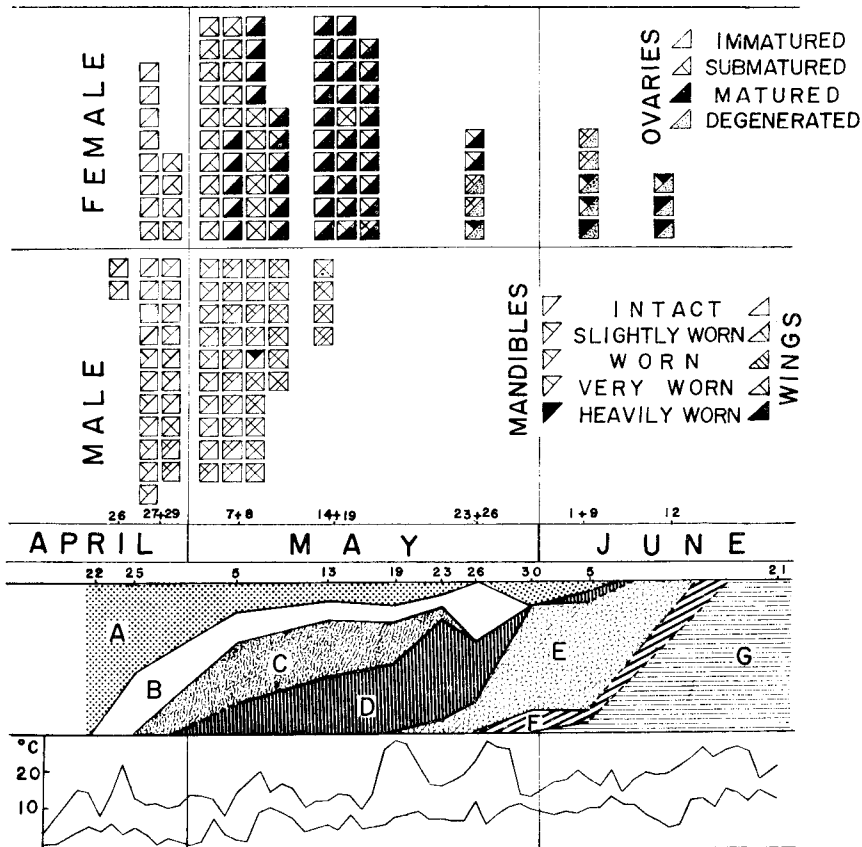


Fig. 1. Phenology and nest development in *Andrena sublevigata*. Top: Phenology based upon sampling on flowers made at intervals of ten days in 1965, showing relative age in each individual. The age is given by mandibular wear and ovarian development in females and mandibular and wing wears in males. Middle: gradual shift of nest contents indicated by percentage ratio based upon excavations in 1966. Numerals indicate dates of nest excavation. A; Burrow without cell, B; Empty cell before provisioning, C; Cell with incomplete pollen ball without egg, D; Egg, E; Feeding larva, F; Prefecated larva, G; Prepupa. Bottom: Maximum and minimum air temperatures in 1966, based upon measurements taken in the Experimental Farm, Hokkaido University.

sity, Sapporo. Most observations given below were also made in the University Campus.

Nest sites observed: Two nest aggregations were discovered in May 1965 in the University Campus and observed in 1965, '66. One was located along the path of about 1.5 m wide, running in the Experimental Nursery between a willow stand (north) and a maple hedge (south). The nests formed a relatively dense aggregation within the range of about 10 m in length, denser in the boundaries, especially the northern one, between the path and the adjoining grassy grounds with relatively loose soil slightly covered with fallen leaves, than in the center of the path with hard and compact ground. Well insulated and prevented from wind, the site was provided with a favorable microclimate. Nests of some other bees, *Lasioglossum duplex* Dalla Torre and several other halictine bees, were found in and near the site and the nesting activities of *A. (Holandrena) valeriana* Hirashima were observed in July. Moreover, the neighboring willows offered a good food source and *A. sublevigata* mainly depended on them in the first half of the flight period.

Another aggregation was found in the ornamental and pharmaceutical plants beds and the path among them in the University Botanical Garden. The site was open, well insulated and relatively less wind owing to the surrounding woods. In this case, too, the nests were more abundant in the beds and margins of paths with loose soil than in the center of the paths.

Adult behavior at nest site: Males usually appear in the later half of April, but in 1966, already on April 8, caused by the warm, sunny and nearly calm weather, which resulted in the sudden rise of air temperature, the maximum soil temperature risen from 3.8 and 2.4°C (5 and 10 cm below surface) on April 7, to 8.3 and 4.6°C respectively. Several males were seen flying in a zig-zag fashion at a few to 30 cm over the soil surface, when air temperatures were 13.0 and 16.5°C (at 150 and 0 cm above surface respectively).

According to Michener and Rettenmeyer (1956), *A. erythronii* starts short flights at air temperature of 50~64°F (=10~18°C) and regular flights at 55~80°F (=13~27°C). They suggested the importance of other factors, surface temperature, soil temperature, wind and sunshine for the flight activities. In *A. sublevigata*, male flights on and near nest sites were observed at air temperature of 11~13°C at 10 cm above the surface. Under lower temperature, they could not fly up, crawling on soil. In the early period of the active season, *A. sublevigata* and other synchronic solitary bees visiting flowers often show the decrease or stop of activities by shading of sunbeam, exhibiting inability to fly, to suck nectar or even to cringe themselves to flowers. This is seen more frequently in andrenids than in other bees, suggesting the higher sensitivity for such temperature change. In general, the critical temperature for flight activities in *A. sublevigata* is regarded about 12~14°C, similar to the case in *A. erythronii*.

The last male flight on nest site was seen on May 5, giving the active period of about one month. During this period, they make every sunny day, especially

midday, zig-zag flights above the ground in and near nest site, between sparse bushes, along branches and stems of willows, apparently searching females. This flight is sometimes interrupted by sun-bathing on sticks or fallen leaves on the ground.

Males dig short overnight burrows (Fig. 3) every day after flight activities in relatively bare and loose ground, never in the ground with accumulations of fallen leaves. The burrow is vertical or oblique, about 2.5~3 mm in diameter and 1~1.5 cm deep. The entrance is provided with the tumulus of 1 cm or less in diameter, distinctly smaller than in female nests. Each burrow mostly contains a single male but the presence of two males was once observed.

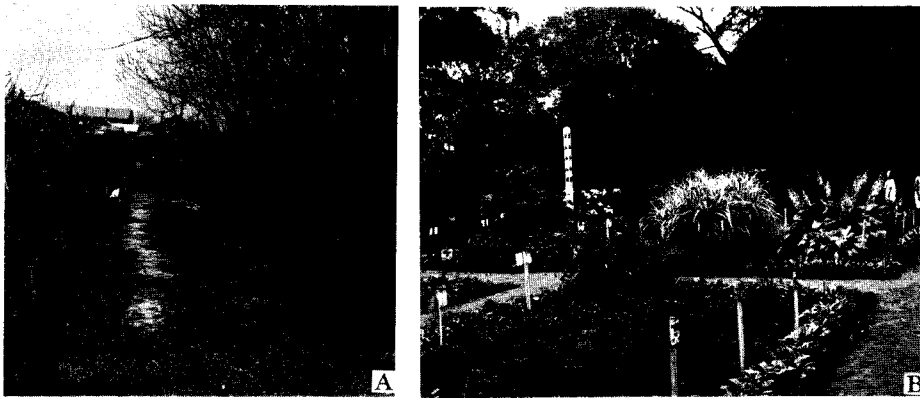


Fig. 2. Nest sites of *Andrena sublevigata*. A: Nest site at Experimental Nursery, University Campus. B: Nest site at Flower beds, University Botanical Garden.

Although not so conspicuous as in females, male mandibles distinctly wear away in the course of the active period (Fig. 1, top), indicating the excavation of overnight burrows. As in most other species, *A. sublevigata* is clearly proterandric. Males appear a little prior to females and disappear in middle to late May. On April 8, '66, several males were first observed, but no female was seen, nevertheless eleven females and one male were sampled by nest excavation on April 11.

The entrances of incipient female nests possess the tumuli distinctly larger than in male burrows. Among six females obtained from nest excavation on April 20, four were already inseminated though the crops of all individuals were still nearly empty. On April 22, the visits of females together with males to willow flowers were observed but no pollen foraging was yet detected. Synchronously several females were seen to fly to and fro above the nest site. Some of them alighted and crawled around on the ground in search of suitable nesting place. At the same time, several males were flying around on the nest site, but no tentative

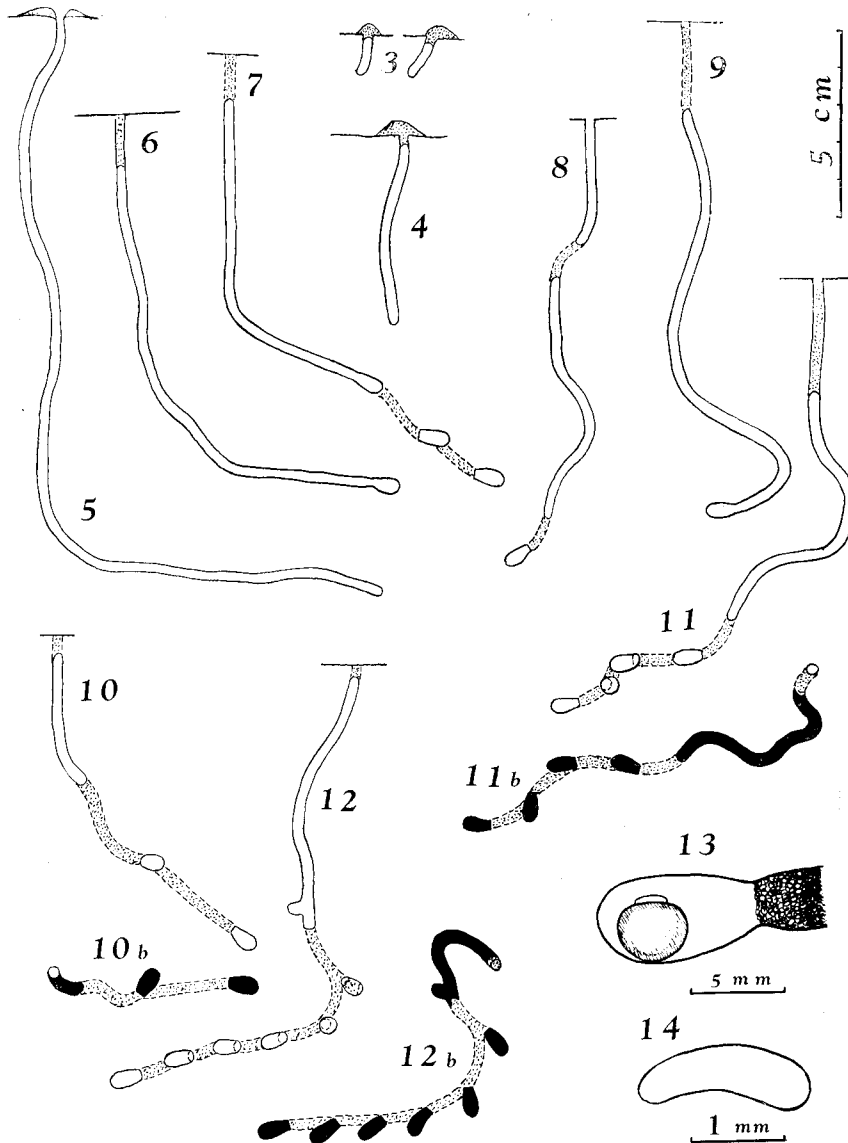
for mating was seen. Seven females were captured and dissected. All possessed nectar and pollen in crops and five were inseminated.

The mating was not observed under natural condition, but one instance was seen within the glass-tube. On October 13, '65, one male and one female were excavated from a nest. They were put in a glass-tube and brought to the laboratory. Activated by higher room temperature, they started walking, then mating. The copulation took place in the manner similar to that in other species, such as *A. erythronii* and *A. watasei* (cf. below). The male pounced on and grasped the female abdomen with legs, keeping the head in the direction same to that of the female. Then he curved the apex of the abdomen ventrally inserted genitalia in female reproductive orifice and released legs in the air, keeping the connection with the female only by means of the abdominal tip. With this posture he began pumping movement several times. During this process the female showed no particular movement. The whole process continued for about three minutes. After the separation of the abdominal tips she pushed away the male by her hind legs. The male tried to pounce on her again but the latter refused him and escaped. Against the repeated interference by the male, she faced to and threatened him by opening her mandibles.

Although the observation was made under an unnatural situation, it is conceivable that females do not accept males immediately after the previous copulation. It is open to the question whether the females accept the copulation more than once during their lives or not. But the second assumption is more likely, because the spermatheca of the female mentioned above was filled with a plenty of sperms.

The speed of nest digging in females depends as in males on various factors, including ability of each individual, temperature, as well as hardness, texture and moisture content of soil. One observation taken on April 22, '66, midday is cited here: One female making zig-zag flights on the nest site was noticed. She repeatedly landed and crawled on the site in search of the suitable spot. Then she crept into the thin layer of fallen leaves and started to dig the burrow. In digging, she loosened soil into particles by biting with mandibles and pushed them behind with fore and mid legs, supporting herself with hind legs and often rotating the body irregularly. About 20 minutes elapsed since the start to dig the burrow to the depth of about 8 mm, comparable to her own body length. Then her body was hidden under the accumulated tumulus.

Nest and cell structure: Females spend the early days of the active season in the shallow vertical burrow without cells (Fig. 4). Later each female deepens the burrow and subsequently makes the distal part, located horizontally or obliquely (Fig. 5). Reaching some depth, she constructs the first cell at the end of the burrow (Figs. 6, 8 and 9), the inside of which is made in oval shape. After finishing provisioning and laying one egg on the top of the pollen ball, the cell entrance is closed with the soil plug. Subsequently the second cell is made at the new end of the burrow proximal to the first cell. It is assumed that the soil shaved off in construction for the second cell may be used for the plug. The same work is



Figs. 3~14. Burrows, cell and egg of *Andrena sublevigata*. 3. Overnight burrows by males. 4~12. Nest burrows of various stages by females in side view. 10b~12b. Ditto, in top view. 13. Cell with egg on pollen ball. 14. Egg.

repeated and in average three to four cells are prepared for each burrow. Frequently the last cell is abandoned without accomplishment, remaining empty with either unworked or polished walls, or with an incomplete pollen ball without egg. Such nest abandonment may be caused either intrinsically by some physiological or psychological factors or extrinsically by the death of the owner, the loss of the nest memory, etc. The differentiation of upper vertical and lower horizontal sections is not always distinct (Figs. 5 and 7). Often both sections can gradually shift from one to the other by a gentle bending or waving of the burrow. Rarely, the burrow is vertical down to the end where cells are also made nearly vertically (Fig. 8). Other intermediate cases are given in Figs. 9 and 10. The nest burrows are made either by new excavation or by repairing of the old nests from which females emerged. The relative abundance of these two instances is not precisely known. In incipient nests, the entrance is hidden under the tumulus, but soon exposed by the gradual disappearance of the latter by desiccation and wind action. The diameter of the entrance is slightly less than that of the main burrow, but not so conspicuous as in most halictine bees.

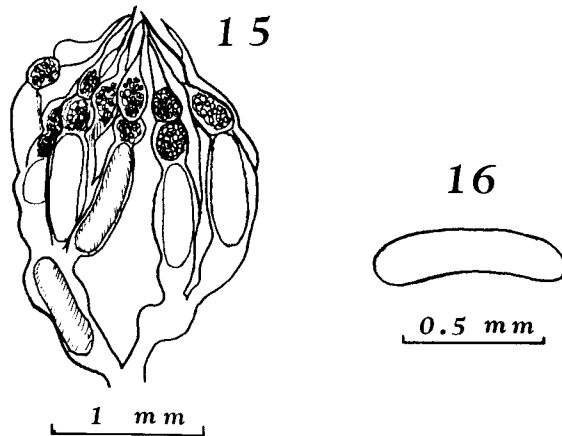
Each cell directly opens to the main burrow, with no intervention of lateral, but seen from above the axis of each cell deviates from that of the main burrow, either alternately (Fig. 11b) or unilaterally (Fig. 12b), forming an acute angle with the axis of the burrow. Seen laterally, cells are either horizontal or inclined downward to 40° . Cells are concentrated at depths of 8~11 cm, in average 9.7 cm (Table 1). The cell is elongate oval and either symmetric or asymmetric, by the bending of the axis (Fig. 12b), seen laterally often flatter above while convex below (Fig. 13). The cell wall is made of two layers as in other species: Very thin, waxy inner layer made of a translucent and polished film and thicker, more loosely cemented outer layer.

Provisioning and development: The trends of the development within nests of this species is shown in Fig. 1, middle, based upon the data of nest excavation in 1966. Since the first appearance of cells on April 25, cells are continuously made till late May. As soon as one cell is made and lined, pollen and nectar are gathered and a spherical pollen ball is prepared.

Judging from the sampling on flowers (Fig. 1, top), flight activities last from late April to middle June, but pollen balls not yet receiving eggs mostly disappear after late May (Fig. 1, middle). Probably foraging activities nearly finish within May. The egg is banana-like, attached to the top of the pollen ball with its whole ventral side. The oviposition is seemingly made throughout May, especially in middle to late period of this month. On June 5, one nest with a cell freshly oviposited was excavated, together with several nests containing various stages of larvae. The preparation of a second nest by some females is plausible by this fact and the absence of fresh females in late May, though still requiring further data. Michener and Rettenmeyer (1956) reported the construction of the second nests in *A. erythronii* and assumed the possibility of such the second nests in other andrenid species, too.

The larval growth seems to be relatively rapid, taking place from late May to middle June. On June 21, all immatures excavated had already reached prepupae. The duration from oviposition to prepupa is assumed to be about one month, based upon Fig. 1, middle, being closely similar to that in *A. candida*, on which Youssef and Bohart ('68) gave 28 days as an average. The prepupal stage is quite long and the pupation takes place in August. On August 30, three pigmented pupae obtained from the cells emerged in the laboratory at the room temperature by the next day. The emerging adults remain and hibernate till the next spring.

Flower visits: Hirashima (1966) recorded the flower visits of *A. sublevigata* to *Brassica*, *Prunus* and *Cardamine*. Sakagami and Matsumura (1967) made an analysis of flower preference of this species in the area where the biological data



Figs. 15~16. Ovaries (15) and egg (16) of *Nomada koelebei*.

mentioned above were obtained, recording the visits to 12 species belonging to seven families. The most predominantly visited plants are willows (*Salix* spp.), *Gagea lutea*, and the European dandelion (*Taraxacum officinale*). The first two species are nearly the exclusive food sources in early spring before the bloom of the European dandelion. In this time, the plants in bloom are still poor, and most foraging activities are mainly directed to willows in the University Campus, while to *Gagea lutea* in the Botanical Garden. It is interesting that *Gagea lutea* is relatively ignored in the University Campus, nevertheless its flowers are quite abundant near the area where the willows are in bloom. After these flowers were over, the bees turn to other flowers such as the European dandelion, rape (*Brassica campestris*) and rosaceous fruit flowers. The difference in flower visits between the two areas studied indicates the plasticity of this species in flower visits as shown by Michener and Rettenmeyer (1956) in *erythronii*.

Including the data taken from other areas, the frequently visited plants are

listed as follows: *Salix* spp., *Gagea lutea*, *Taraxacum officinale*, *Brassica campestris*, *Potentilla fragarioides*, *Prunus*, *Malus*, and *Pyrus*.

Parasite: It was confirmed that *Nomada koelebei* Cockerell was a labor parasite of *A. sublevigata*. During the flight season of the host bee, this parasitic bee was often seen to fly in a zig-zag fashion above the nesting sites and to invade in the burrows. When the host was in the burrow, the invader departed after a brief pause. But, in the absence of the host, she stayed in the burrow for a few minutes or more, probably laying her egg on the pollen ball in the open cell. One female of *N. koelebei* was obtained from the cell of *A. sublevigata* excavated on October 13, '65, and one male in the same way on August 23, '66. One female was caught on May 5, '65, when she was flying around above the host nest site and her ovaries were examined (Figs. 15 and 16). The right ovary was consisted of four ovarioles while the left one of five, showing an asymmetry often known in parasitic bees. The largest ovarian egg was banana-shaped, 0.2 mm wide and 0.7 mm long, distinctly smaller than the host egg, reflecting the mode of life (*cf.* Iwata and Sakagami 1967).

Andrena (Gymnandrena) watasei Cockerell

A. watasei is a common, relatively large-sized species (body length: ♀ 12~14 mm, ♂ 10~11 mm) flying from May to July in Hokkaido (Fig. 17, top). The species is characterized by the relatively prolonged flight season than in other andrenid bees, extending to above two months or more. From the gradual change of ovarian condition and of mandibular wear given in the figure, the species is certainly monovoltine as described by Hirashima (1964), and so far as the flight activities are concerned, proterandric as in *A. sublevigata*. Males appear in early May prior to females, seen to repeatedly fly around through the definite course among sunny bushes or the grassland in zig-zag fashion. Males disappear by the late June, while females are seen to July. No information was obtained regarding the life span of each adult individual.

Nest sites: A nest aggregation was observed at the Experimental Nursery, Hokkaido University in 1966 (Fig. 18). Since this aggregation had already been discovered by Dr. S. F. Sakagami in 1959, it had continued at least for seven years in the same place. The aggregation was located stretching over an abandoned weedy area and a path along the margin of a larch stand, not so distant from the nest site of *A. sublevigata* mentioned above. The nests were more abundant in the weedy area with relatively thick vegetation consisting of timothy, orchard grass and plantain growing to 30~50 cm in height, than in the path. In total, 31 nests were found within the range of 1.5×2.0 m sq. In the most concentrated part nine nests were counted within 50 cm. sq. The nest site was exposed to the sun only in the morning, shaded since 10:00 by the larch stand in the southern side. The soil was moderately packed with the humus deposit of 5~10 cm thick above the fine loam layer. Most nest entrances were found on the

shady ground among or by grasses (Fig. 19).

Another small aggregation consisting of less than 10 nests was discovered within the Experimental Nursery, on the grassy ground shaded nearly throughout day time under thick foliage. It is therefore conceivable that this species prefers the shaded ground for nesting and tends to form nest aggregation.

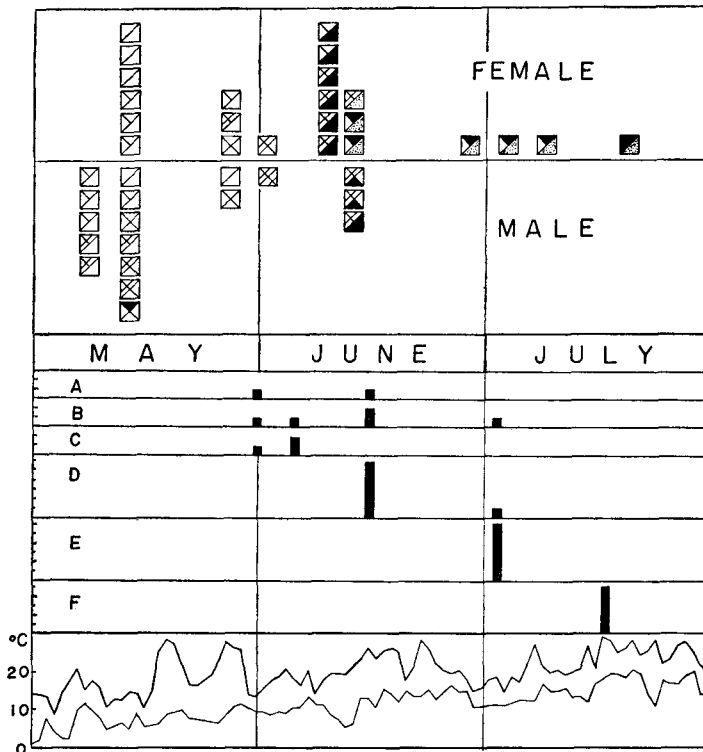


Fig. 17. Phenology and nest development in *Andrena watasei*. Top: Phenology based upon ten days periodical sampling on flowers made in 1965, showing relative age in each individual by mandibular wear and ovarian development in females and by mandibular and wing wears in males. (Explanations in Fig. 1). Middle: Gradual shift of nest contents indicated by individual numbers, based upon excavations in 1966. A; Burrow without cell, B; Cell with incomplete pollen ball without egg, C; Egg, D; Feeding larva, E; Predefecated larva, F; Prepupa. Bottom: Maximum and minimum air temperatures in 1966, based upon measurements taken in Experimental Farm, Hokkaido University.

Nest and cell structure: In 1966 nests of *A. watasei* were periodically excavated from May 31 to June 16. The nest of the species belongs to the stationary branched nest type (*heterodalous* in Malyshev 1935) with cells connected

with the main burrow by means of laterals. As given in Table 1, every nest element is largest among the three species recorded in the present paper, corresponding to the body size. In the early phase, the entrance was accompanied with the tumulus, 1~2 cm high and 5 cm or more in diameter, consisting of yellowish brown loam brought out from the deeper soil layer contrasting with the dark surrounding surface. Later the loam tended to be packed hardly after getting moisture, making the discovery of entrances relatively easy. The entrance, either open or plugged with loose soil mass, was slightly constricted in most cases (Table 1).



Fig. 18. Nest site of *Andrena watasei* at Experimental Nursery, University Campus.

The main burrow consists of two sections, vertical section descending from the entrance to the depth of about 10~15 cm and horizontal section, as long as or shorter than the former, starting from the end of the vertical section and running subhorizontally or obliquely for about 4.5~13 cm. In most nests, the vertical

section is more straight and the junction between two sections is more distinct than in *A. sublevigata* (Fig. 20~22), except one nest in which two sections were not sharply distinguished for each other (Fig. 23). Both vertical and horizontal sections are often partly filled with loose soil even in active nests (Figs. 21, 22), as in *A. erythronii*.

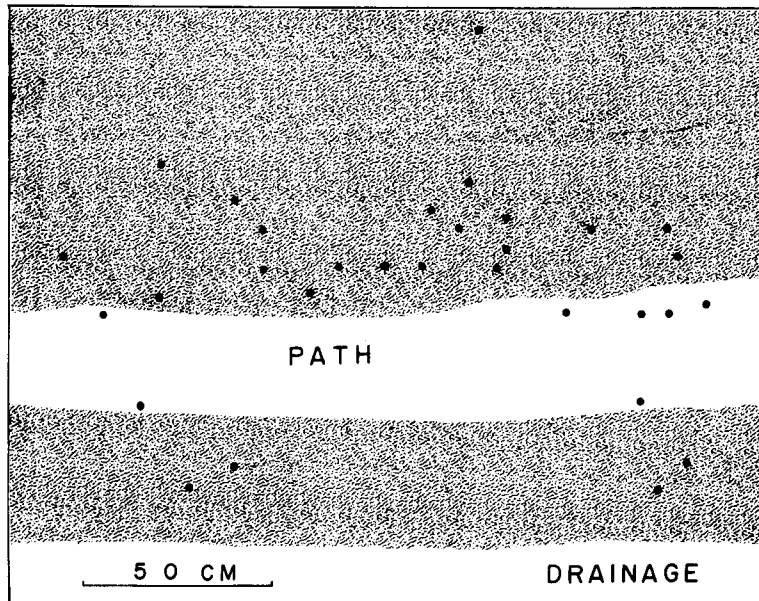


Fig. 19. Distribution of nest burrows of *Andrena watasei*.

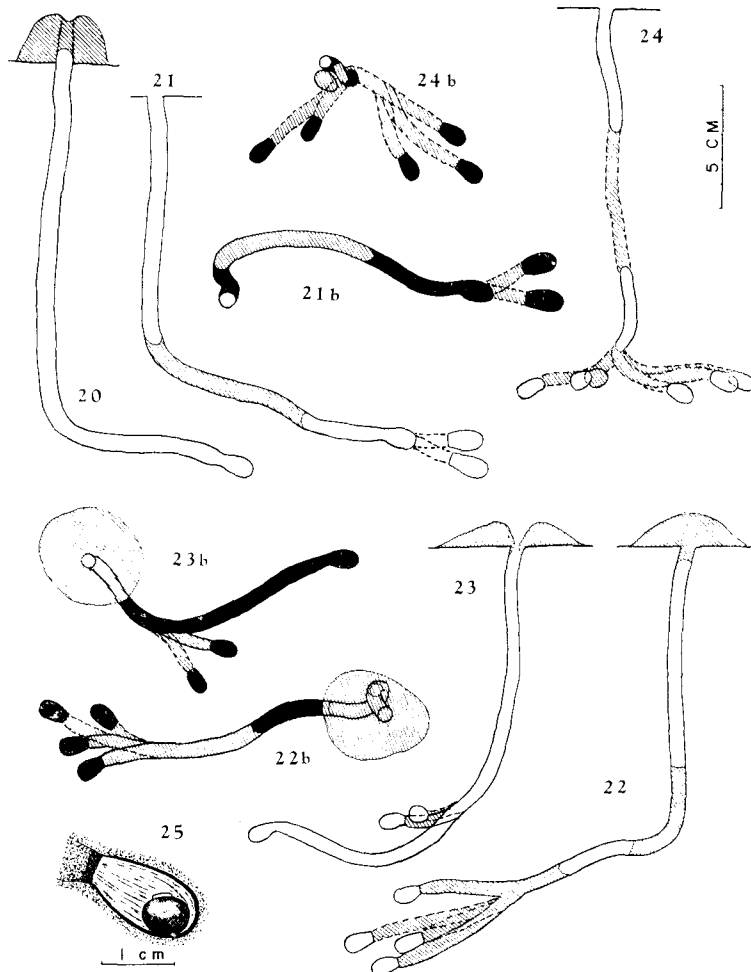
From various points of the horizontal section one to five relatively long laterals or branches issue, each of which leads to one cell, though in one case the cell was located at the middle of the lateral (Fig. 21). The laterals are usually slightly narrower (5~6 mm), than the main burrow (6~7 mm). In one nest without horizontal section (Fig. 24), the laterals issued directly from the end of the vertical section. In top view, laterals with cells diverge one another taking a fan-like arrangement (Figs. 21b~24b), in the maximum diverging up to 110° (Fig. 24b). Seen laterally cells are more inclined downward than laterals, from 10 to 45°.

The cell is oval as in other *Andrena*, the neck narrower than the lateral, 4~5 mm in diameter. The cell wall consists of two layers, as in other species. The inner surface is polished, occasionally longitudinally finely grooved (Fig. 25).

The pollen ball is spherical, slightly flattened, placed near the end of the cell (Fig. 25), with the size variable as in Table 1, mostly moderately firm, though in a single case, soaked with liquid, probably nectar, like as reported in *A. parathor-*

acica (Hirashima 1962), *A. candida* (Youssef and Bohart 1968) and *A. ovina* (Malyshev 1926).

The egg is elongate, less curved than in *A. sublevigata* and other species, laid on the top of the pollen ball, with the long axis parallel to the longitudinal axis of the



Figs. 20~25. Nest burrows and cell of *Andrena watasei*. 20~24. Nest burrows in side view, b. Ditto in top view. 25. Cell with egg on pollen ball, carved with fine grooves.

cell. After oviposition, cell openings and laterals are filled with compact soil so that often difficult to trace the connection with the main burrow.

Brood development and mating: Fig. 17, top shows the gradual aging of adults

sampled as in *A. sublevigata* (Fig. 1, top), periodically on flowers, shown by ovarian condition and mandibular wear in females and mandibular and wing wears in males. Fig. 17, middle shows the gradual shift of nest contents based upon five successive excavations made on May 31, June 5, 15, July 2 and 16, 1966. The seasonal shift of brood rearing activity is recognized by combining these two results. The nest construction and provisioning start mostly in late May, and oviposition takes place mostly in early June. The general trend is similar to that in *A. sublevigata*, with some differences in the duration of each stage.

On July 16, all immatures were the full grown larvae or prepupae. Most immatures may reach the prepupae during July. The duration of prepupal stage seems to be short, contrary to that in *A. candida* which lasts for 14 days in average (Youssef and Bohart 1968) and *A. sublevigata* (cf. above). On August 8, all immatures were white pupae. The duration of the pupal stage is likely within a month, considerably shorter than in other monovoltine species, i.g. *A. sublevigata* (two months or more) and *A. erythronii* (about five months). On August 23, slightly pigmented pupae were excavated and they all emerged in the laboratory within six days. In late September, fresh adults of both sexes were observed within cells. Therefore this species hibernates, as in *A. sublevigata*, as adults in the emerging cells till the next May.

Mating was once observed on a leaf of coltsfoot on May 4, 1965. A flying male pounced on a female sun-bathing on the leaf. Mating behavior was generally similar to the other andrenid species. Another case was observed on the flower of the European dandelion or *Taraxacum officinale*. These incidental observations suggest that mating is made on plants than on nesting grounds.

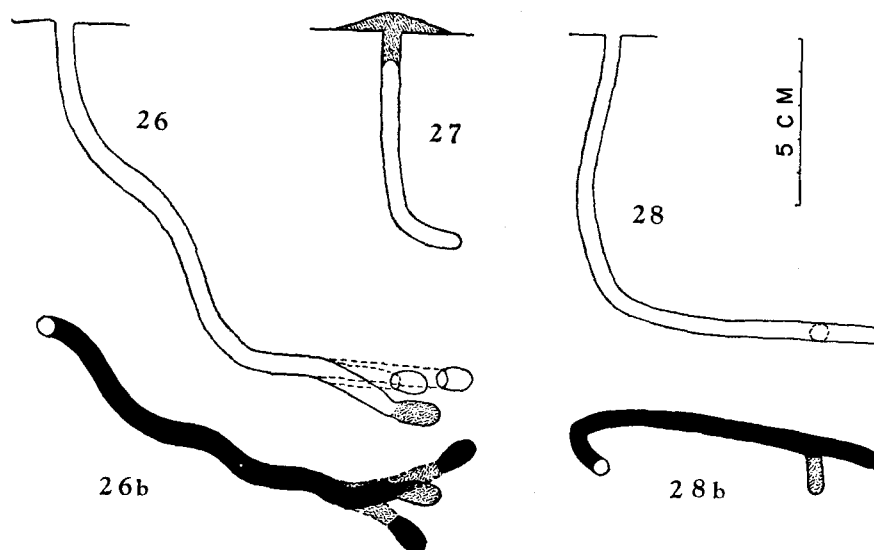
Flower visits: The flower visits of this species has been recorded as follows: Miyamoto (1960, Sasayama, Hyogo Pref.): 12 flower species (belonging to 11 families); especially *Taraxacum platycarpum* and *Brassica campestris*; Hirashima (1964, probably mainly in Kyushu); frequent visits to *Brassica* and *Ranunculus*; Sakagami and Matsumura (1967, Sapporo): 21 species (12 families) in females, and 12 (9) in males; Matsumura and Munakata (1969, Hakodate): 13 (6) in females and 3 (3) in males. In the last two papers, the European dandelion is recorded as the most frequently visited flower in both sexes. Matsumura and Munakata (1969) observed a seasonal shift of flower species visited. The species seems to be plastic to flower preference as in *A. sublevigata*.

Andrena (Cnemidandrena) seneciorum Hirashima

A. seneciorum is a medium-sized species (body length: ♀ 10–11 mm, ♂ about 9 mm), having abundant brown to fuscous hairs on the body. The adults are found in rather hilly to mountainous areas in North Japan, and one of the latest *Andrena* species, collected from late July to early September. On August 12, 1969, the nests were discovered and excavated by the writer at Yukomanbetsu, a hot spring settlement situated at 1,070 m in altitude on the way to Mts. Taisetsuzan.

The locality belongs to the subalpine zone, with forests characterized by *Picea jezoensis*, *Abies sachalinensis* and *Betula erminii* as dominant trees and undergrowth of *Sasa kurilensis*. Nesting site was the open ground with short and sparse grasses and herbs at a waste place slightly inclined to S-W direction in front of a lodge.

Among three nests examined, one (Fig. 26) was the old burrow containing hibernated adults and the other two (Figs. 27, 28) were still under construction, each by a female apparently soon after emergence. Although this species appears from late July or early August at lower altitude, its active period must delay and shorten at higher subalpine zone with cooler and unstable climate. The nest type, recognized by the old burrow given in Fig. 26 alone, is similar to that



Figs. 26~28. Nest burrows of *Andrena seneciorum*.

in *A. watasei*, that is, stationary branched with the dimensions given in Table 1. Among three cells, two were closed with soil plug and contained fresh females still before departure, and the third cell was filled with loose soil. A fresh male was found near the bottom of the lateral. It is unknown whether this male emerged from the cell filled with soil or entered into the burrow from the outside.

This species specially prefers composite flowers blooming in summer to autumn, which occupy 12 out of all 14 flower species visited, with predominantly visited ones such as *Picris hieracioides*, *Solidago serotina*, *Erigeron annuus*, *Aster glehni*, *Senecio palmatus*, and *Anaphalis margaritacea*.

Discussion

The nesting habits and some biological notes of three species mentioned in the present paper accord in general to the information so far published on the bionomics of *Andrena*. Here is given some comments on the nest structure.

The nests of *Andrena* are considered to be of rather primitive type among various bee nests (Michener 1964). According to the classification of the bee nests by Malyshev (1936), the *Andrena* nests so far recorded are classified into three types: 1) Branched or *Heterodalous*¹⁾, 2) Linear or *Pallodalous*, 3) Linear-branched or *Paradalous*. The first type is known in most European and Nearctic species so far studies, i. g. *A. ovina*, *A. erythronii* and *A. candida*, and in the Japanese species, *A. prostomias*, *A. watasei* and *A. seneciorum*. The second type is represented by five species from Japan, *A. knuthi*, *A. japonica*, *A. parathoracica*, *A. astragalina* and *A. sublevigata*. The last type is reported only in two species, European *A. bimaculata* and Japanese *A. japonica*.

In *A. sublevigata*, cells are arranged in a line along the main burrow, with the longitudinal axes diverging alternately or unilaterally from that of the burrow. Probably this condition suggests the phase transitional from stationary branched to completely linear. The similar arrangement is seen in *A. bimaculata* with paradalous nests. The nest of *A. candida* is of the branched type but rather approaching to the linear type by the possession of very short laterals. In *A. (Holandrena) valeriana* Hirashima (Matsumura, unpublished) nesting in the open grounds, the nest type is linear and the axes of cells approximately tend to coincide with that of the main burrow. Consequently there exists a gradual change from typically stationary branched to completely linear type, exhibited by the series, *A. watasei* type → *A. candida* type → *A. sublevigata* type → *A. valeriana* type. Finally the linear-branched nest is assumed to be derived from the linear nest. This change may be advantageous because the bees need not to newly excavate a second or a third nest. It is plausible that this type appears facultatively in the same species. As to *A. japonica*, Hirashima (1962) recorded the linear type, while Okumura (1964) the linear-branched one.

Although the nest types of *Andrena* remain still in primitive conditions, the gradual change assumed above indicates an evolution in relation to the labor economy. The same change from branched to linear type is suggested also in halictine nest architecture (Sakagami and Michener 1962), indicating an interesting parallelism between two dominant soil dwelling bee groups. Within the limit of the information so far known, no definite relation between nest type and taxonomic grouping (at subgeneric level) is still obtained, but further accumulation of comparative data is required to clarify this problem.

1) The nest of *A. (Cryptandrena) viburnella* Graenicher, recorded by Stephen (1966) goes to this type, but differs from all other *Andrena* nests so far recorded in nearly vertical main burrow, laterals issuing rectangularly and sharply bending and vertically oriented cells.

Summary

The nesting habits of three andrenid bees, *Andrena (Micrandrena) sublevigata* Hirashima, *A. (Gymnandrena) watasei* Cockerell and *A. (Cnemidandrena) seneciorum* Hirashima, were observed in Hokkaido, Northern Japan. The outline of habits and some numerical data on nest structure are summarized in Table 1. All species are monovoltine, and the first two species hibernate as adults in cells.

Nest type of *A. sublevigata* is linear (allodalous), consisting of a main burrow, separated into upper vertical and lower horizontal section. The cells are arranged linearly along the horizontal section, with the axes divergent from that of the main burrow. Nest type of *A. watasei* and *A. seneciorum* is stationary branched (heterodalous), consisting of a main burrow and several laterals, each of which ends by a cell. It is assumed that linear arrangement was derived from stationary branched type through the labor economy as in halictine bees.

References

- Friese, H. 1882. Beitrag Zur Biologie der *Andrena pratensis* Nyl. (*ovina* Kl.). Ent. Nachr. 8: 317-319 (Not directly accessible).
- 1923. Die europäischen Biene (Apidae). Walter de Gruyter and C., Berlin and Leipzig, 456 pp.
- Hirashima, Y. 1962-66. Systematic and biological studies of the family Andrenidae of Japan. 1962. Pt. 1. Biology. J. Fac. Agr., Kyushu Univ. 12: 1-20. 1964. Pt. 2. Systematics, 3. Ibid. 13: 39-69. 1966. Pt. 2. 7. Ibid. 14: 89-131.
- Iwata, K. and J. F. Sakagami. 1966. Gigantism and dwarfism in bee eggs in relation to the modes of life, with notes on the number of ovarioles. Jap. J. Ecol. 16: 4-16.
- Kawamura, M. 1957. On the nest of *Andrena prostomias* Pérez. Gensei 5: 19-20 (In Japanese).
- Malyshev, S. 1926. The nesting habits of *Andrena* F. Trav. Soc. Nat. Leningrad 56: 25-78 (In Russian).
- 1935. The nesting habits of solitary bees. A comparative study. Eos 11: 201-309.
- Matsumura, T. and M. Munakata. 1969. Relative abundance, phenology and flower preference of andrenid bees at Hakodateyama, Northern Japan (Hymenoptera, Apoidea). J. Fac. Sci., Hokkaido Univ., Ser. VI, Zool. 17: 106-126.
- Michener, C. D. 1964. Evolution of the nests of bees. Amer. Zool. 4: 227-239.
- and C. W. Rettenmeyer. 1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera, Andrenidae). Univ. Kansas Sci. Bull. 37: 645-684.
- Miyamoto, S. 1960. Flower-visiting habits of fourteen species of andrenid bees (Biological studies on Japanese bees XIV). Kontyû 28: 65-86 (In Japanese).
- Okumura, T. 1964. Biology of *Andrena japonica* Smith. The life Study (Fukui) 8: 53-57 (In Japanese).
- Sakagami, S. F. and T. Matsumura 1967. Relative abundance, phenology and flower preference of andrenid bees in Sapporo, North Japan (Hymenoptera, Apoidea). Jap. J. Ecol. 17: 237-250.

- and C. D. Michener 1962. The nest architecture of the sweat bees (Halictinae). A comparative study of behavior. 135pp. Univ. Kansas Press, Lawrence.
- Stephen, W. P. 1966. *Andrena (Cryptandrena) viburnella*. I. Bionomics. J. Kansas Ent. Soc. **39**: 41-51.
- Youssef, N. N. and G. E. Bohart 1968. The nesting habits and immature stages of *Andrena (Thysandrena) candida* Smith (Hymenoptera, Apoidea). J. Kansas Ent. Soc. **41**: 442-455.