Systematic and biological studies of the family Andrenidae of Japan (Hymenoptera, Apoidea) Part Ⅰ. Biology

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Systematic and biological studies of the family Andrenidae of Japan (Hymenoptera, Apoidea)

Part I. Biology*

Yoshihiro HIRASHIMA

INTRODUCTION

This paper is the result of a study of the systematics as well as the biology and ecology of the bees of the family Andrenidae of Japan. Since the publication of the first report of my paper entitled *Descriptions and records of bees of the genus* Andrena *from Eastern Asia*, in 1952, interesting facts have been accumulated to our knowledge on the bees of that family. Up to the year 1951, only 18 species of *Andrena* have been known from Japan. From 1952 to 1960, I have described 21 species and subspecies as new. Now 58 species belonging to 21 subgenera will be recorded in this paper. Of these, 20 species and 4 subgenera are considered to be new. It is my great pleasure to receive friendly collaboration from Prof. Wallace E. LaBerge of the University of Nebraska in describing of these new subgenera.

At the same time, the investigations of the nesting habits as well as the flower preferences of the bees of Japanese Andrenidae have also been conducted. The results will be presented in the Part I of this paper (*biology*) and in the section of *flower records* given at the end of the species description.

ACKNOWLEDGMENTS

My thanks are due first of all to my teacher, Dr. Keizô Yasumatsu, Professor of Entomology of Kyushu University, without whose neverfailing support and kind guidance this paper could not have been presented. Ever since my first report on *Andrena* published in 1952, he

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has followed my work with special interest, inspiring enthusiasm and helpful criticism. For his kind guidance throughout these years I owe him a great debt of gratitude.

To the late Professor Teiso Esaki I am deeply indebted for his interest and kind guidance upon my study.

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Dr. O. W. Richards of Imperial College, London, has kindly helped me in preparing the notes on the type specimens of *Andrena* which were found in the British Museum (Natural History).

Dr. L. Berland of the Paris Museum has kindly helped me, through the favour of the late Prof. Esaki, in comparing the specimens in question with the types of Pérez's species which are preserved in his museum.

To Prof. Wallace E. LaBerge of the University of Nebraska and Dr. R. W. Grünwaldt, München, I owed to their criticisms upon the interpretation of certain subgenera and species.

For the gift and lending of the specimens, I am deeply indebted to the following entomologists: Dr. S. Asahina, of National Institute of Health, Tokyo, Mr. T. Edashige, of Ehime University, Mr. A. Fukuda, Hachinoe, Aomori Pref., Mr. N. Fukuhara, of Agricultural Experiment Station, Tokyo, Mr. S. Hisamatsu, of Ehime University, Mr. R. Ishikawa, of Kyushu University, Dr. K. Kamijo, Hokkaido, Mr. H. Kamiya, of Kyushu University, Mr. T. Kifune, of Tottori University, Mr. S. Kimoto of Kyushu University, Dr. T. Kobayashi, of Agricultural Experiment Station, Tokushima, Mr. K. Komatsu, Osaka, Dr. Y. Kurosawa, National Science Museum, Tokyo, Mr. Y. Maeta, of Shinshu University, Dr. R. Matsuda, of the University of Kansas, Prof. S. Miyamoto, of Kyushu University, Dr. S. Miyamoto, of Hyogo University of Agriculture, Mr. Y. Miyatake, of Kyushu University, Dr. K. Morimoto, of Forestry Experiment Station, Tokyo, Dr. R. Morimoto, of Research Laboratories, Takeda Chemical Industries, Osaka, Dr. Y. Murakami, of Horticultural Experiment Station, Hiratsuka, Mr. H. Nagase, Tokyo, Mr. K. Nohara, of Agricultural Experiment Station, Yamaguchi, Mr. T. Saigusa, of Kyushu University, Dr. S. F. Sakagami, of Hokkaido University, Dr. M. Sasakawa, of Kyoto Prefectural University, Mr. K. Sato, of Department of Agriculture, Tokyo, Dr. T. Shirôzu, of Kyushu University, Mr. M. Takahashi, of National Institute of Health, Tokyo, Dr. K. Takeuchi, of Takeuchi Entomological Laboratory, Kyoto, Prof. C. Takeya, of Kurume University, Mr. I. Togashi, Ishikawa, and Mr. H. Yamamoto, of Institute of Public Health, Fukuoka. Above all, Mr. Ishikawa has kindly offered to me many interesting specimens.

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Mr. Y. Maeta, of Shinshu University, has kindly helped me in observation of the biology of certain species of *Andrena*.

I am further indebted to Dr. M. Shimizu, of Kyushu University, for identification of the plants of pollen and nectar sources.

Thanks are also due to Drs. K. Morimoto and Y. Murakami for illustrations of the male genitalia and associated structures.

Biology

Although the nesting habits of a number of European and American species of *Andrena* have been reported (Perkins, 1919; Friese, 1922; Malyshev, 1926; Bishoff, 1927; Emeis, 1955; Michener and Rettenmeyer, 1956; Linsley and MacSwain, 1959; etc.), no information is available for Japanese species other than the observations on the nest construction and habits of *Andrena prostomias* Pérez. They have been reported by Kawamura (1957, 1961). Flower records have been presented for 13 species of *Andrena* and 1 species of *Panurginus* (Miyamoto, 1960). Although Miyamoto conducted an extensive investigation, her observation has been limited to the local flora.

Basing upon the importance of the bees of the family Andrenidae to the pollinations of some crop plants and fruit trees, I have conducted a series of observations on the biology as well as the flower preference of them. The results pertaining to the biologies of some species will be given briefly in the following chapters. Reports on the wild bees, including Andrenid and Panurgine bees, as an agent of the pollination of some crop plants and fruit trees of economic importance in Japan will be published separately from this paper.

I. Biology of *Andrena* (*Chrysandrena*) *knuthi* Alfken

On the morning of June 14, 1959, when I was collecting the insects on Mt. Hikosan, Prov. Buzen, Kyushu, I had a good chance to find an aggregation of the nests of *Andrena* (*Chrysandrena*) *knuthi* Alfken. It was consisted of hundreds nests which were nested primarily on the edge of a pathway (Fig. 1), where the ground was covered by several kinds of grasses and *Miscanthus sinensis*. Many females were found

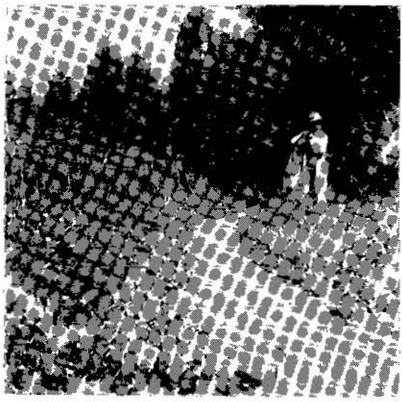


Fig. 1. Nesting site of *Andrena (Chrysandrena) knuthi* Alfken found on Mt. Hikosan, Kyushu. (Photo. on June 14, 1959, by Y. Maeta.)

when returning to the nests with a large amount of yellow pollen load on her hind legs. Then, observations of the female activities around the burrows as well as the excavations of the nests, in cooperation with Mr. Y. Maeta, were conducted there.

Female activities around burrows

The activities of a number of females around their burrows were observed on two successive days. Most of the females gathered pollen on both the observation days. One of the records of the foraging flights of the females is shown below (June 14, 1959, fine).

E: Entering burrow with pollen loads.
L: Leaving burrow.

E (09 : 49) ------ L (09 : 53) -·-·- E (10 : 13) ------ L (10 : 17) -·-·- E (10 : 34) ------ L (10 : 38) -·-·- E (11 : 00) ------ L (11 : 06) -·-·- E (11 : 46)

Another record is as follows:

E (10 : 11) ------ L (10 : 17) -·-·- E (10 : 42) ------ L (10 : 46) -·-·- E (11 : 10) ------ L (11 : 15) -·-·- E (12 : 14)

As can be seen, duration of a foraging trip varies, in the former, from 17 to 38 minutes and in the latter, from 24 to 59. It is also clear that females of *knuthi* remained from 4 to 5 minutes in her own nest for taking dry pollen off from her legs. The excavations of nests reveal the fact that females accumulate the pollen loosely at the bottom of the cell during the period of provisioning and, then, she makes a pollen ball, probably with the admixture of nectar, after a sufficient amount of pollen has been accumulated. Since the pollen collecting apparatus of *knuthi* is considerably well developed (see systematic portion of *Chrysandrena*), the pollen load adhering onto it is very large (Fig. 2). It is noteworthy that since the species of *Andrena* collect and carry their pollen dry (Hodges, 1952), an amount of pollen loads carrying by the females varies from the species to species in accordance with the degree of the development of the pollen collecting apparatus.

The plants of pollen and nectar sources of *knuthi* were not studied at that time. However, on May 20th, 1950, when I visited Mt. Hikosan, with Mr. R. Ishikawa, we found many females collecting pollen from the flowers of *Picris hieracioides* which were in full bloom. *Andrena* *knuthi* was the sole bee which was found on the flowers of *Picris hieracioides* at that time. Judging from this record, it seemed that females of *knuthi* were collecting pollen from *Picris* which were blooming near-by the nesting site. On the other hand, it is concluded from my observations during the past ten years that females of this species commonly associate with the flowers of Compositae, Rosaceae and Ranunculaceae. Miyamoto (1960) recorded 16 species of pollen plants belonging to 8 families for this species. According to these records, it is clear that *Andrena knuthi* is polylectic.

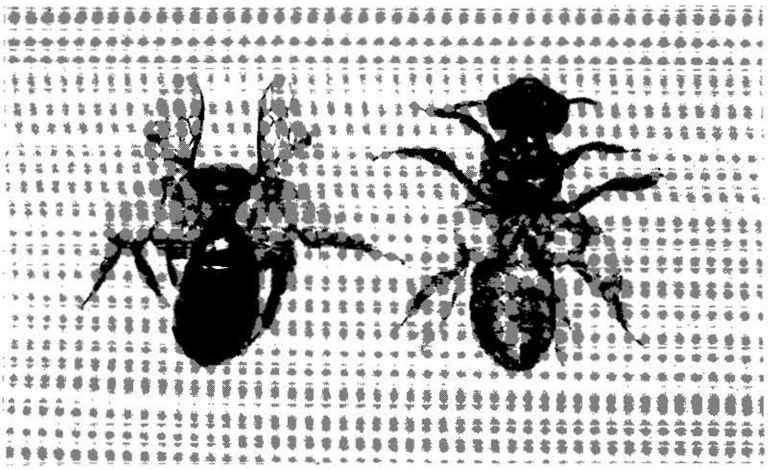


Fig. 2. Females of *Andrena* (*Chrysandrena*) *knuthi* Alfken showing the pollen loads adhering onto the hind legs and propodeum.

When returning with a pollen load the females usually fly directly to the burrow. On rare occasions they alight on grasses or the ground near-by the burrow and remain for a short while before entering the burrow. Then, they fly and reach the entrance of own burrow on wings, not on legs. Flight away from the burrow was usually direct.

The burrows were closed with earth in the afternoon. The earth of plug was brought up from the interior of burrow and it was placed just below, or occasionally more than 1 cm below the entrance.

On the next day, June 15, a successive observation was made from 06 : 45. Some of the nests were seen already open at that time, but many were still closed. Around 07 : 30, a few females departed for the first trip. Opened burrows were increased in number toward 08 : 15. At 08 : 16, a female was seen returning from her first trip to the nest with a pollen load. At that time, many females were still remained in their own burrows which were open long before. About 09 : 00, females leaving or entering burrows were gradually increased in number.

The first trip to the flower was usually accompanied with the orientation flights. After opening the burrow the female remains just within the entrance until ready to leave. By and by, she leaves the burrow on legs. As soon as the tip of her metasoma gets out of the entrance, she turns round and face to the entrance. After a short excitement, she flies aloft. The orientation flight is indicated by the zig-zag flights, facing to the entrance, at the lower altitude and the circling flights at higher altitude. The flights increase the speed in accordance with the increase of the altitude, and then females fly away to the flowers.

Distribution of burrows

It was noted that the burrows of *Andrena knuthi* distributed much more densely in the area which was covered by the grasses than in the bare ground. In a given space of 60 by 60 cm, 29 nests were counted on June 15. Of these, only 2 nests were found in the bare ground. The majority of nests counted was found either in the area which was heavily covered by the grasses or in the marginal area of the path-way in which sparse grasses were grown. It is shown in Fig. 3.

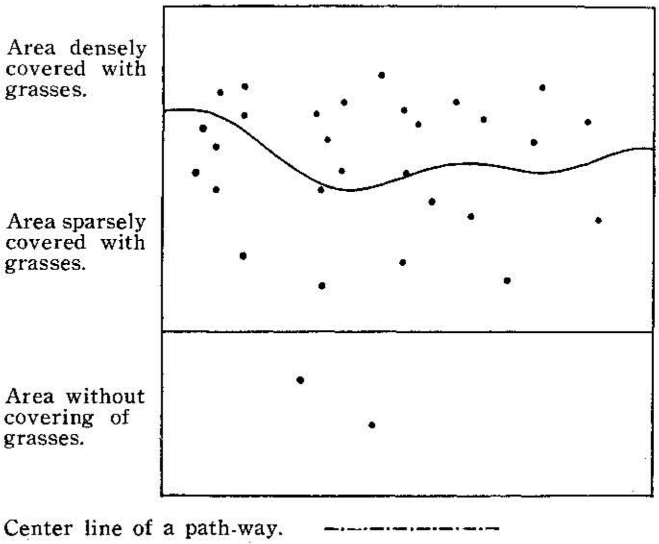


Fig. 3. Distribution of the burrows of *Andrena* (*Chrysandrena*) *knuthi* Alfken at Hikosan (June 15, 1959). (cf. Fig. 1.)

Nest structure

The nests of *Andrena knuthi* are 15 to 30 cm deep. The entrance of the burrows is narrowed; it is about 3.5 mm wide. The burrow, which is round and about or less than 5 mm in diameter, runs nearly vertically into the soil, and then curves irregularly. The terminal part of the burrow which runs to the cells is usually sub-horizontal (Fig. 4, A).

Andrena knuthi nests not only in the horizontal ground but also in the vertical cliff. I happened to find several nests of the latter situation on Abura-yama, Fukuoka City, on June 2, 1959. One of the nests excavated at that place is shown in Fig. 5.

The cells are placed nearly horizontally or slightly more slanting; they are about 10 mm long and 6 to 6.5 mm wide. The interior of the cell is polished and coated with a thin membrane. As shown in Fig. 4, the cells are not clustered but placed separately in a line (end by end). Since the burrows were excavated so closely each other that I failed to trace the whole cells associated with a burrow. Near the end of the cell, a pollen ball is placed, which is almost exactly spherical, and about 4 to 4.5 mm in diameter (Fig. 4, c, d). The egg (Fig. 4, c, d and Fig. 6), which is slightly less than 2 mm in length, is a slightly curved cylinder, deposited on the top of the pollen ball. The ovary of the nesting female is shown in Fig. 6.

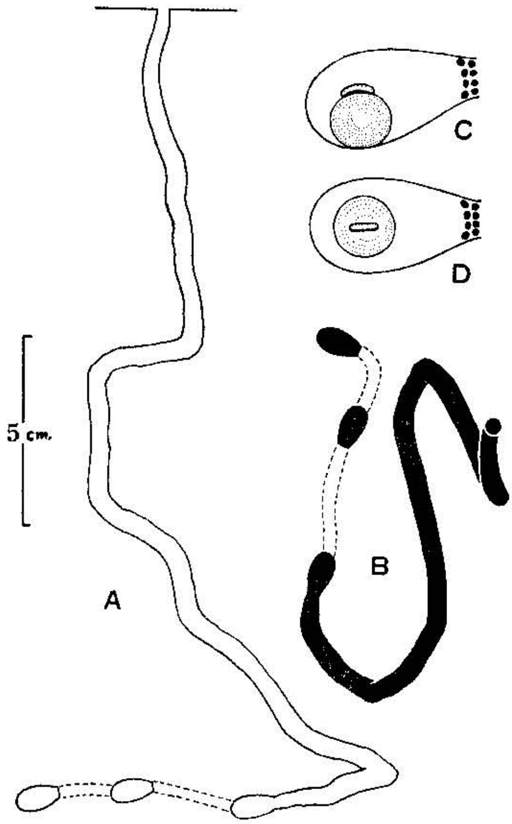


Fig. 4. Nest of *Andrena* (*Chrysandrena*) *knuthi* Alfken. A and B: Burrow, lateral and top views; C and D: Brood cells, lateral and top views.

Development

The egg period was not acertained but it is supposed that it lasts a week or so. Probably the larvae consume the pollen provisions within a month. *Andrena knuthi* passes the summer in the stage of the full grown larva which pupates at about the end of summer or in the autumn. It overwinters as adults, still inside the brood cells, as in *Andrena parathoracica* Hirashima which will be described below. As far as known, the vernal species of *Andrena* pass the winter as adults.

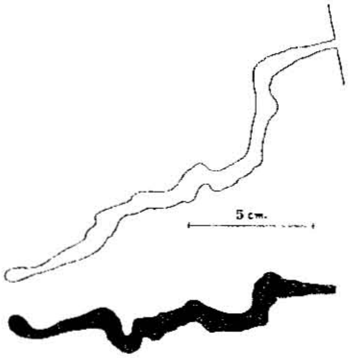


Fig. 5. Nest of *Andrena* (*Chrysandrena*) *knuthi* Alfken which was found on the vertical cliff.
Above: Lateral view;
Below: Top view.

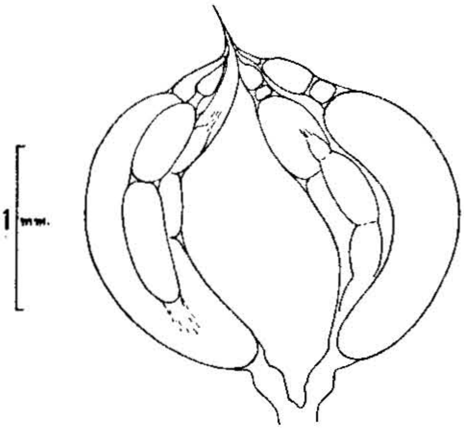


Fig. 6. Ovary of the nesting female of *Andrena* (*Chrysandrena*) *knuthi* Alfken.

2. Biology of *Andrena japonica* (Smith)

Andrena japonica is not a vernal species but the flying season of it is primarily limited to June. This species is one of the commonest insects which are found on the flowers of carrot in Kyushu. So far as my observation goes, this species nests in the bare ground of the wilders or in the marginal portions of the path-way in the cultivated or semi-cultivated areas. Not a few nests of this species, which were located here and there along the edge of a path-way in Kashii, Fukuoka (Fig. 7), were found in 1958 and again in 1959, on which the following investigations were made.

Nest structure

The burrow, which is about 7 mm in diameter, of *Andrena japonica* runs obliquely into the soil and curves irregularly until the brood cells which are placed end by end at the end of main burrow (Figs. 8, 9). Like *Andrena knuthi*, the burrows are simple, lacking the lateral branches before the cells. The cells are situated obliquely (neither

Fig. 7. Nesting site of *Andrena japonica* (Smith) at Kashii, Fukuoka. (Photo. on May 12, 1959.)

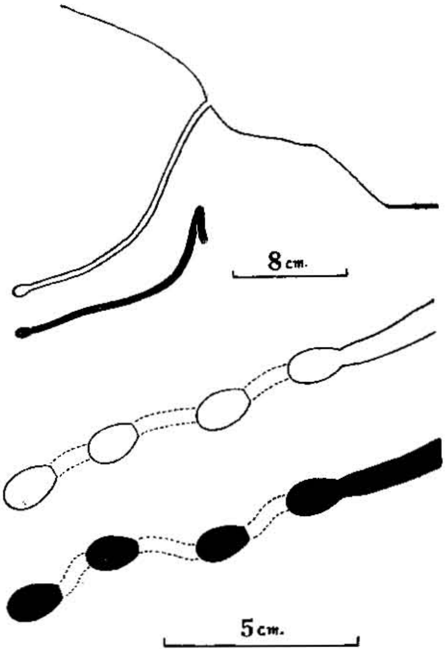


Fig. 8. Burrow and nest structure of *Andrena japonica* (Smith). The black spaces are those of top views.

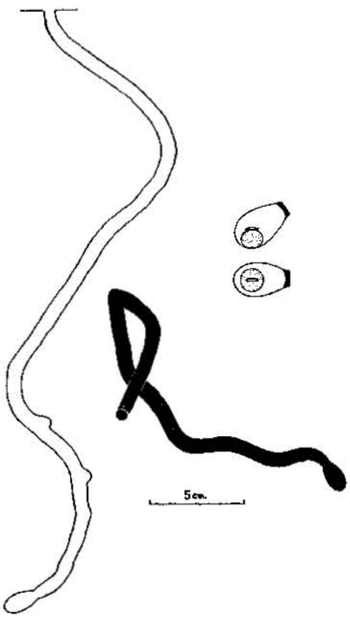


Fig. 9. Burrow and brood cell of *Andrena japonica* (Smith).

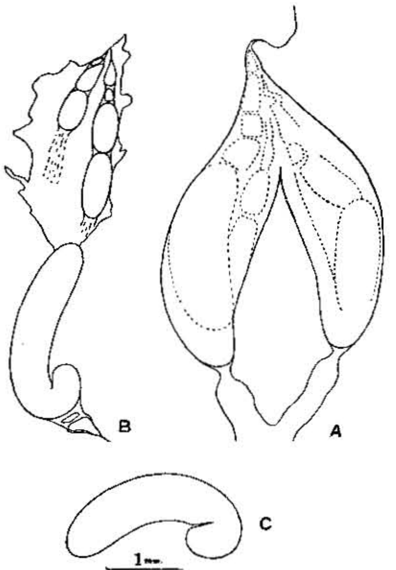


Fig. 10. Ovary of the nesting female of *Andrena japonica* (Smith). A: General view; B: Ovariole, cup open; C; Mature egg.

horizontally nor vertically), polished and coated with a transparent membrane internally; they are 14–15 mm long and 8–9 mm wide.

At the bottom of the cell, a pollen ball is placed, which, like *Andrena knuthi*, is almost exactly spherical (Fig. 9). It is 5 to 6 mm in diameter. Unfortunately I could not observe any of the deposited egg on the pollen ball. As the results of the dissections of the nesting females of *Andrena japonica*, it is proved that the mature egg is about 2 mm in length. It is noteworthy that one end of the egg (probably the head of embryo) is uncinate as shown in Fig. 10. The ovary of *japonica* is enclosed with a thick, white membrane, through which the ovarioles, unlike *Andrena knuthi*, can not be clearly recognizable. Such condition is also observed in *Andrena parathoracica* Hirashima as stated and illustrated below.

3. Biology of *Andrena* (*Gymnandrena*) *parathoracica* Hirashima

So far as my investigation goes, this species is not very rare but the distribution of it is very local. The nesting site of this species was first discovered by Mr. Toyohei Saigusa of Kyushu University on Abura-yama, Fukuoka City, in early summer of 1957. It was found on the nearly vertical bank of the field which forms the edge of a path-way as well. Since then, an aggregation of nests were observed in consecutive years. A full account of the biology of this species has not yet been obtained, but the brief descriptions of the nest construction as well as the ovary of the female are given herewith.

Nest structure

The soil in which the burrows of *Andrena parathoracica* were excavated was sandy so that it seemed that the excavations of the burrows by the female bees were easy. It is significant that the burrows of this species are rather simple, as shown in Fig. 11, not so much curved as in *Andrena knuthi* Alfken or *Andrena astragalina* Hirashima which nests in the harder ground.

Because of the large size of the female of this species the burrows are large, 8–9 mm in diameter. At the end of burrow, several separated brood cells (usually four) are placed end by end as in most of the species of *Andrena* (Linsley, 1958). It is clear that it is the terminal cells that are first finished. As this is done, it is assumed that the end of burrow is lined and shaped to form a cell (1st cell); the burrow is closed with earth for a short distance after the 1st cell having been finished, and then the 2nd cell is lined and shaped. The cells are 15–16 mm long and 9–10 mm wide. They are oblique to nearly vertical in situation.

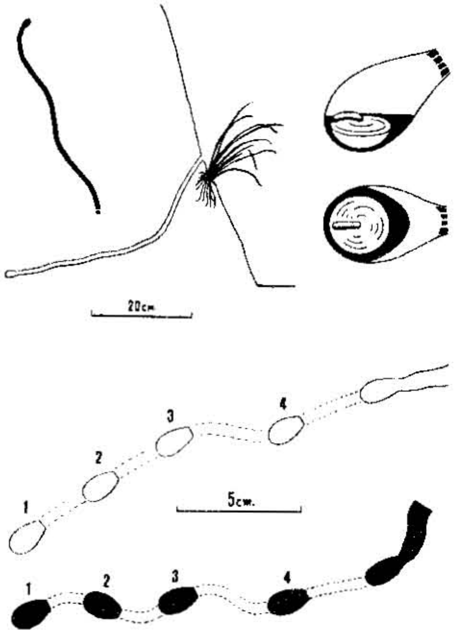


Fig. 11. Burrow and nest structure of *Andrena (Gymnandrena) parathoracica* Hirashima. For explanation see text.

The provisions of this species are characteristic. The load is hemispherical in shape, surrounded with a transparent liquid (Fig. 11) which is probably due to the hygroscopic properties of honey (Malyshev, 1936). Like other Andrenid bees, the cells are polished and coated by a membrane internally.

Ovaries of nesting females

The ovaries of the nesting females of *Andrena parathoracica*, as illustrated in Fig. 12, are fully enclosed with a thick, non-transparent membrane. Like *Andrena japonica*, it is rather difficult to distinguish either the ovary or ovarioles through the membrane. At least a mature egg is contained in one ovary. So far as I am aware, such a condition of the thickened and non-transparent membrane is found only in some species of *Andrena*.

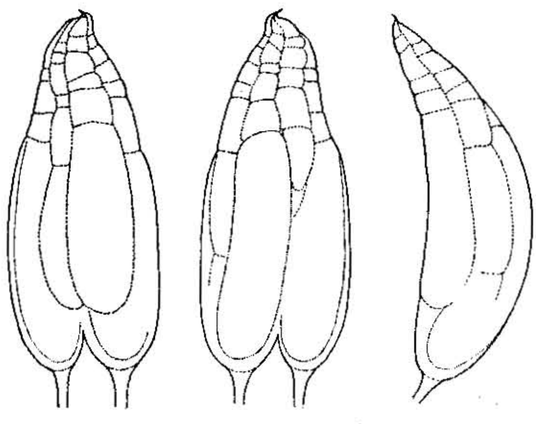


Fig. 12. Ovary of the nesting female of *Andrena (Gymnandrena) parathoracica* Hirashima. From left to right: dorsal, ventral and lateral views.

4. Biology of *Andrena* (*Plastandrena*) *astragalina* Hirashima

This species is one of the vernal species of *Andrena* which visit the flowers of *Brassica* and *Astragalus*. Although *astragalina* is not a very rare species the distribution of it is very local. I had a good fortune to find a number of nests of this species on the edge of a path-way in a semi-cultivated area of Kashii, Fukuoka City, in the spring of 1957, upon which the following investigations were made.

Female activities around burrows

One of the distinctions of the female behaviours around the burrows of *Andrena astragalina* is the return flight to the burrows. The flights of *astragalina* are rapid and powerful. When returning with a pollen load, the female usually alights on the trees or the ground in the general nesting site before entering her own burrow. Reposing for a few minutes, she flies and hovers here and there, usually facing to her own burrow and about or more than 50 cm apart from it, at an altitude of a few centimeters from the ground. Finally she flies at an ultra-low altitude, directly to the entrance of the burrow and then enters quickly.

According to the observations made in the afternoon of April 18, 1958, the duration of time remained within the burrow varied from 21 to 29 minutes. Comparing with the case of *Andrena knuthi* Alfken, it is clear that the time spent within the burrow in the course of the provisioning is considerably long. Females spent from 43 to 50 minutes for a foraging trip. It seemed that females gathered pollen from the flowers of *Brassica* which were in full bloom in the neighborhood of the nesting site.

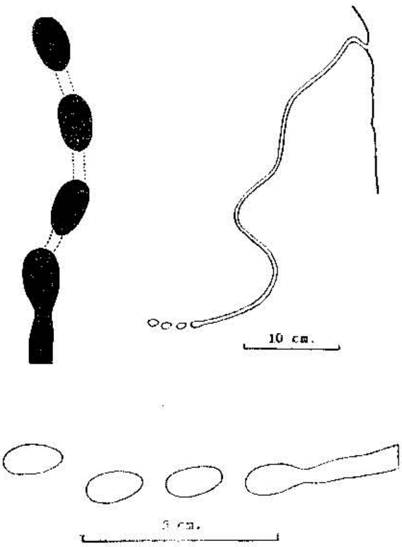


Fig. 13. Burrow and nest structure of *Andrena* (*Plastandrena*) *astragalina* Hirashima.

Nest structure

The soil in which the burrows of *Andrena astragalina* were excavated was clayey and very hard. The burrows were sinuate and deep (Fig. 13); they are about 8 mm in diameter. When they were found on the horizontal ground the burrows were excavated obliquely into the soil. The burrows of *astragalina* were found not only in the horizontal ground but also in the vertical face of the soil. In the latter case, the burrows ran obliquely upwards for a short distance, then curved downwards. The terminal parts of the burrows were situated subhorizontally as seen in *Andrena knuthi*, *parathoracica*, etc.

The brood cells of *astragalina* were found about 60 cm in depth or more deeper part of the ground. They were placed end by end (Fig. 13), as usual for the species of *Andrena*.

5. Biology of *Panurginus crawfordi* Cockerell

This is a single species of *Panurginus* occurring in Japan, and one of the most abundant bees associated with flowers of *Brassica*. The females range from 7.5 to 8.5 mm and males from 6 to 7 mm; they are rather slender and shining black, having the yellow clypeus in the male. The distribution of this species is constricted to the western half of Japan. In these areas, they fly early in spring, having one generation in a year. The nests of *Panurginus crawfordi* were found nearly always in bare area of waster land or semibarren area of firm (Fig. 14). Prof. Yasumatsu has told me that he observed a large aggregation of the nests of this species in the playground of

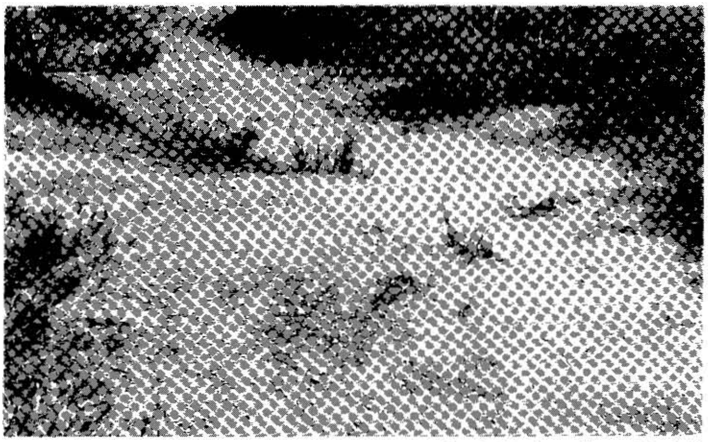


Fig. 14. Nesting site of *Panurginus crawfordi* Cockerell at Kashii, Fukuoka. (Photo. on June 15, 1959.)

Kyushu University, Fukuoka, about fifteen years ago. They are observed frequently occurring gregariously in a rather small area, but sometimes only a few nests were found. More or less large aggregations of *Panurginus crawfordi* were found in the bare clay-ground of the hill at Kashii, Fukuoka, on which the present observations were conducted from the spring of 1958.

Overwintering

The most interesting fact in the life-history of *Panurginus crawfordi* lies one the feature of overwintering. This species overwinters in the larval stage (Fig. 15). The body of mature larvae is protected by so hard skin that it is quite stable to alterations in the physical environ-

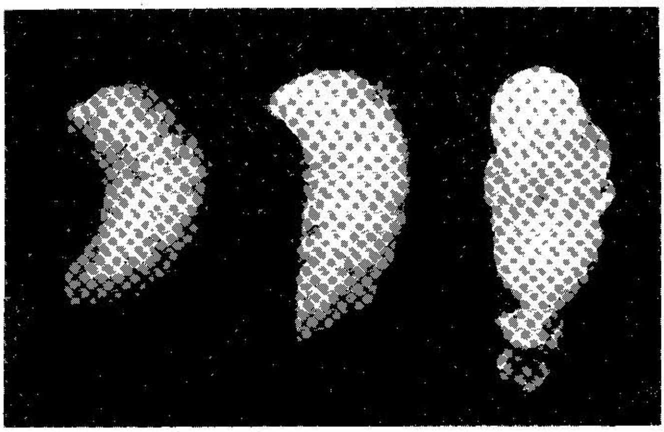


Fig. 15. Larvae and pupa of *Panurginus crawfordi* Cockerell. Left: Larva, hibernating form; Middle: Larva, just before pupation; Right: Pupa, just pupated.

ment, very contrasting to the case of *Panurginus melanocephalus* (Cockerell) just reported by Linsley and MacSwain (1959). Therefore, the laboratory rearing of larvae of *Panurginus crawfordi* is very easy.

The cells in which mature larvae oversummer as well as overwinter are placed in the depth of 5 cm on an average from the surface of the ground, as described below. From midsummer to winter, however, a number of cells of *Panurginus crawfordi* are frequently found nearly at the surface of the ground or but a few centimeters under the surface. This is caused by the erosion of heavy rain-falls in the rainy season (mid June to mid July) which covers the western half of Japan annually. Thus, the cells of this species are usually placed nearly directly to the changes of weather, especially to the fluctuation of temperature. In a long daylight of midsummer, for example, the surface of the bare ground is considerably highly heated and dried. It is of great interest to note that larvae of *Panurginus crawfordi* live safely through a considerable long period (from about end April to next early spring) in these cells in rather bad conditions making a striking contrust to the great majority of Andrenid bees which nest deeper in the ground.

Pupation and emergence

Pupation takes place in early spring. On March 18, 1959, several males of *Panurginus crawfordi* were found flying over the nesting site. This is the first record for this year. The emergence of laboratory-reared adults followed by about five days. On March 25, a week later from the first appearance, hundreds of males and a number of females were observed flying busy here and there near the surface of the ground. At this time, some burrows were found already excavated. On successive days more females (and males probably) appeared until the end of March. These records nearly agree with these of the previous year.

Male activity

At the early period of the flying season, males overnight in burrows from which they emerged, or in soil cracks, or in small shelters newly burrowed by them every night. About mid season, males were not found in these burrows or soil cracks at night; they spend the night on the grasses, flowers, etc.

Although mating of this species has not yet been observed but intertwining pairs were found sometimes both on the flowers of *Brassica* and on the ground of the nesting site.

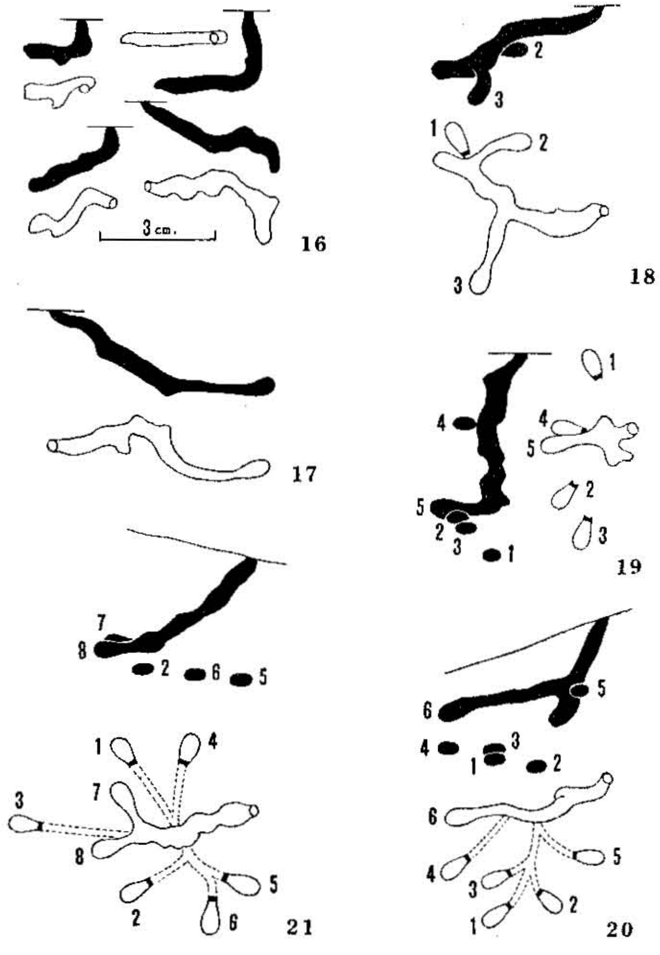
Males are active each day on the flowers of *Brassica* throughout the season. They fly from flower to flower, for sucking nectar and for females; a number of males usually are observed on the flowers of *Brassica* until late afternoon on successive fine days.

Nest structure

The burrows of *Panurginus crawfordi* are found principally in the bare ground. Since it is gregarious, burrows are usually found closely placed. In the mid season of 1959, 18 burrows were observed in the space of 30 by 50 cm; the distances of them vary from 2 to 12 cm.

The burrow shaft runs vertically or obliquely into the soil for a short distance, usually less than a depth of 7 cm. There are no regularity; they are principally sinuous and irregulary branched to a cell (Figs. 16–21). They vary in diameter from 3 to 6 mm. As the soil is excavated it is accumulated around the entrance as a tumulus. The entrance is about 2.5 mm in diameter; it is usually loose and friable. Therefore, it is frequently observed that the entrances of burrows are so liable to close lightly by the tumulus that the females returned to the burrows with pollen face to some difficulty in entering burrows for a short while.

The cells are about 8 mm long and about 4.5 mm wide. They are placed nearly horizontally, in the depth of 5 mm on an average. The wall is polished and coated by a transparent membrane internally. The pollen ball is about 3 mm in diameter, somewhat condensed dorso-ventrally. It is placed at the end of the cell, on which an elongate, dorsally curved egg is deposited horizontally along the long axis of the cell.



Figs. 16-21. Burrows and nest structures of *Panurginus crawfordi* Cockerell. All drew in the same scale. Black figures show lateral aspects; white top views. For other explanations see text.

Completed cells are plugged with soil at the neck. The lateral burrows to the cells which are irregularly branched from the main shaft are also plugged with soil whatever the cells have been completed.

In the afternoon the entrances of burrows are closed daily by the female both during nest construction and provisioning as in the great majority of Andrenid and Halictid bees. The plug is composed of more or less moist soil brought up from the burrow; it is placed usually just below the entrance in about 2 mm thick.

The results of the excavations of nests at the early period of nest construction were shown in Figs. 16 and 17, representing the styles of construction of the shafts. The burrow shown in Fig. 17 which was excavated on April 17, 1959, was associated only with a single cell, the interior of which was coated by a membrane but not provided with pollen. There is an evidence that the lateral burrow to the first cell run from the end of the shaft.

Another excavations of the nests on the same day, April 17, 1959, reveal the progress of the provisioning of the cells. One of the results is indicated by a burrow with 3 associated cells: 1 cell (1st cell) with egg, 1 cell (2nd cell) not provided with pollen but coated by a membrane internally and 1 cell (3rd cell) polished roughly, neither provided with pollen nor coated by a membrane (Fig. 18). As seen in Fig. 18, the latter two cells (2nd and 3rd cells) are connected by own lateral burrow which runs from the main shaft independently. Then it is assumed that these features clearly demonstrate the procedure of nest construction of this species.

Successive excavations of the nests which were conducted on April 28 and May 1 demonstrate the development of the nest (Figs. 19-21). For example, a burrow with 8 associated cells which was excavated on May 1, 1959, is shown in Fig. 21: 2 cells (1st and 2nd cells) with full-grown larvae, 3 cells (3rd to 5th cells) with rather large to medium-sized larvae, 1 cell (6th cell) with very young larva, 1 cell (7th cell) with egg, and 1 cell (8th cell) without egg but with half-made pollen ball. Thus, the order of the cell construction is clearly indicated in spite of the irregular location of the cells.

A burrow with 10 associated cells was excavated on April 28, 1959, and it was the biggest one so far observed.

Diurnal activities of the female

In the mid season, the daily flights for pollen provisioning of *Panurginus crawfordi* usually begin about 09:00 and last approximately three hours. As a whole, the burrows are closed every afternoon as stated before. A single flight for pollen and nectar requires 20 to 40 minutes. The females of *Panurginus crawfordi* mixed pollen and nectar on the flowers and they carry such pollen loads as moist, large masses on the tibiae and basitarsi of the hind legs. Entering burrow with pollen loads, the female bee spends about 4 minutes in her nest.

The first departure of the female from her own nest for pollen and nectar starts with an orientation fly every day. The female leaves the entrance with her head first. Then she turns and faces to the entrance. After a very short excitement she flies above the entrance, facing and sub-circling rather slowly it for a short while at the distance of 5 to 10 cm. She gradually increases altitude and widens the circles. Finally she leaves with a few wide and irregular flights over the area.

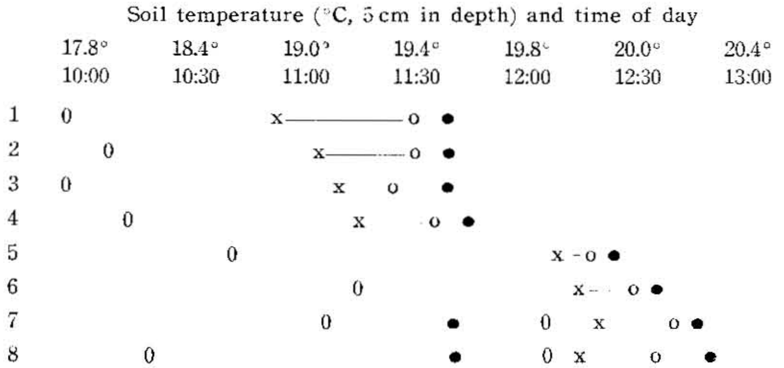


Fig. 22. Unusual activities of 8 females of *Panurginus crawfordi* Cockerell which were observed on April 17, 1959 (weather condition: fine).
0: nest open, x: departure for the first trip with an orientation fly,
o: arrival without pollen loads, ●: nest closed

On very rare occasions, a population of females of this species was observed simultaneously to stop gathering pollen all day long notwithstanding the suitable weather condition for flight. For example, on April 17, 1959, it was observed with great surprise that none of the females in an observation area were returned to their nests with pollen loads after the sole flight in the day. Some of the records are shown in Fig. 22. There was a heavy rain-fall in the previous night, and it is assumed that this is one of the serious reasons why they stopped foraging.

Habits of parasitic fly

The most important parasite of *Panurginus crawfordi* is a small Dipterous fly belonging to the family Muscidae (undetermined). The adult flies of this parasite are not rare at the nesting site of *Panurginus crawfordi*, watching and waiting on the ground for a chance to pursue the females of their hosts. When a female of *Panurginus crawfordi* returns with pollen loads onto the nest, a fly flies above and follows after the bee by a distance of about 5 cm and about a few centimeters downwards. Upon this pursuit, bees fly unusually or occasionally alight upon the ground apart from the nest and exert herself to escape from the fly, but usually bees alight upon the nest and enter into the burrow without any special attention to a pursuer. The bee and pursuer alight upon the nest nearly at the same time, and the fly faces to the entrance of nest about a few centimeters apart from it and watches it in the state of repose until the bee departs the nest for next foraging flight. As stated before, females of *Panurginus crawfordi* spend about 4 minutes in the nest to leave the pollen loads. During this time, the fly sits quite motionless. As soon as the bee flies away, the fly walks to the entrance of the nest and looks into the burrow for a moment. Then the fly turns about and enters quickly into the burrow backward. The fly spends about a minute in the burrow and probably she deposites eggs into the cell in progress. It is of interest to observe that the fly appears *slowly* from the inner part of the burrow after oviposition, as if she is contented with her success.

The larvae of the fly feed on the pollen ball and grow rapidly. It is frequently observed after the excavation of the nests that two or more of larvae of the fly live simultaneously on a pollen ball together with a larva of *Panurginus crawfordi*. Under that circumstances, the pollen ball become slushy. This condition of the pollen ball seems to be unsuitable for the larva of *Panurginus crawfardi* and it dies before long. The full grown larvae of the fly pupate in the soil out of the cell.

Parasite other than the fly

No species of parasitic bees on this species has not been found. In late spring of 1959, I dug out from the nests of *Panurginus crawfordi* two larvae of Coleopterous parasite which seems to belong to the species of *Zonitis*. Unfortunately it is not yet determined.

Summary to the nest construction of *Andrena* and *Panurginus*

Bishoff (1927, p. 224) stated that "In der grossen Gattung *Andrena* herrscht, soweit bisher bekannt, eine rechte Einförmigkeit im Nestbau." This is true so far as my observations are concerned. Thus, the nest of *Andrena* is always dug in the ground and consists of a main burrow with short lateral tunnels leading to the brood cells. The cells are placed usually subhorizontally to subvertically (see Figs. 4, 8, 9, etc.), not as "nearly or quite vertically" as stated by Lanham (1949, p. 190). The cells are usually lined internally with a very thin coating of transparent membrane, and provided with a pollen cake on which an egg is deposited. The pollen cake is, as already seen in previous chapters, quite spherical in *Andrena (Chrysandrena) knuthi* Alfken, but it is condensed dorso-ventrally in *Andrena (Gymnandrena) parathoracica* Hirashima. It is of interest to note that the pollen cake of *Andrena parathoracica* is ringed with liquid honey just as in *Andrena ovina* Klug* reported by Malyshev (1926). So far as I know, this nature is only rarely observed in *Andrena.*

A chain of brood cells is, usually less than five in number, found at the end of the lateral tunnels in the nests of *Andrena.* In *Andrena parathoracica*, for example, usually four cells are placed in a line as shown in Fig. 11. On rare occasions, however, only a single cell is constructed at the end of the lateral tunnels in certain species of *Andrena.* Bohart (1952, p. 112) shows the nest of *Andrena subaustralis*† in such a condition and Kawamura (1961, p. 21) that of *Andrena prostomias* Pérez. The latter named species belongs, so far as my investigation goes, to a new subgenus which will be described in Part II of this paper and is considered to be primitive in the hierarchy of *Andrena.* As can be seen from Figs. 16–21, interestingly, the nest of *Panurginus crawfordi* Cockerell belongs to the same type. Rozen (1958, p. 43) shows the nests of *Nomadopsis anthidius* (of the type of *Panurginus crawfordi*) and *Nomadopsis euphorbiae* (of the type of most of *Andrena*), both of which belong to the subfamily Panurginae in the family Andrenidae. Thus, now it is clear that there exist two types of nest construction among the bees of Andrenidae, even in the genus *Andrena.*

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* In the opinions of E. Stöckhert (1930) and F. K. Stöckhert (1954), *Andrena ovina* Klug is a synonym of *Andrena vaga* Panzer. I keep a female of European *Andrena vaga* Panzer which was determined by Mr. J. P. van Lith. Interestingly, *Andrena vaga* Panzer is a good representative of the subgenus *Gymnandrena*, to which our *Andrena parathoracica* Hirashima belongs.

† According to Lanham (1949), *Andrena subaustralis* belongs to the subgenus *Cryptandrena* which is now recognized as *Bythandrena*. *Bythandrena* is closely related to *Gymnandrena*, and Dr. W. E. LaBerge of the University of Nebraska is in the opinion that it is a synonym of *Gymnandrena* (in personal communication).