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What are Stingless Bees, and Why and How to Use Them as Crop Pollinators? — a Review —

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Abstract

The efficiency of insects as crop pollinators depends on their biological characteristics in relation to the crop and the environment in which they are needed. For glasshouse pollination in Japan, stingless bees are potentially promising pollinators for the following reasons: they are harmless to beekeepers and glasshouse workers, they visit a wide range of crops (polylecly), they are tolerant of high temperatures, they are active throughout the year, they can be transported easily, and they do not pose an environmental risk by escaping and invading natural habitats as they would not survive the Japanese winter. There are still, however, some limitations to using stingless bees in such areas, one of which lies in how to improve methods for propagating and maintaining the colonies throughout the year. To address this problem we suggest the development of a new type of hive box.

Discipline: Crop production / Horticulture
Additional key words: beekeeping, meliponiculture

Introduction

Stingless bees are social bees which lack a functional sting. They store honey and pollen, and are sometimes called stingless honey bees[17]. Since they occur in perennial colonies in tropical and subtropical climates, it is impossible for them to survive naturally throughout the cold season in countries with a temperate climate such as Japan. Considering that these people-friendly and ecosystem-friendly bees could be used as crop pollinators, we introduced colonies of several species from Australia and other countries, and investigated methods for keeping and multiplying hives.

The general biology of stingless bees has been described by various authors[17,23,28], and pollination by stingless bees in tropical areas has been reviewed recently[9]. Most of the research, however, has been conducted in the areas where the bees live. Very little work on using stingless bees introduced from overseas has been performed in Japan, much less from the practical pollination point of view. Sakagami introduced the concept of domestication of stingless bees first into Japan[22]. Maeta et al. imported 7 species of stingless bees, *Trigona minangkabau, T. moorei, T. itama*, from Southeast Asia; *Nannotrigona testaceicornis, Plebeia droryana, T. angustula, T. barocoloradensis* from Brazil, with a view to testing them as pollinators of strawberries and published a note stating that *N. testaceicornis* was the most effective one and that economical fruit production could be maintained by the introduction of colonies into glasshouses[15].

In this paper we describe the use of insects as crop pollinators in Japan, and also the potential of the stingless bee, *T. carbonaria*, from Australia to be kept and utilized successfully as pollinators under glasshouse conditions.

Status of pollinator utilization in Japan

Where no pollinators are available, many crops need hand or mechanical pollination. Multiple use of insecticides and expansion of single cropping, both of which have been conducive to the development of modern agriculture, have also led to the decrease of natural pollinator populations. In addition, cultivation under structures, such as glasshouses or greenhouses, where no rain, wind, or natural pollinators could be expected, has been disseminated in response to the rising demand for fruits and

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vegetables. These agricultural conditions have stimulated the demand for efficient manageable pollinators for crops.

Three species of insects have had a great impact on crop pollination recently in Japan.

The first is *Osmia cornifrons*, a solitary bee used since 1945 and now essential for the pollination of crops, especially of apples. The pollinating ability of *Osmia cornifrons* on apple is considered to be much higher than that of the honey bee. *Osmia cornifrons* is so efficient at pollinating crops that it was introduced into the USA in 1977 for small orchards on the East coast, and into Denmark for greenhouse crops. Its life cycle is very simple: the mated female makes a series of cells in the tubes it selects for nesting in spring; when foraging trips occur, each cell is filled with a honey pollen mixture on which it lays an egg; a new adult emerges within the nest in early autumn and overwinters therein; she appears out of the nest and mates and then makes foraging trips for a new nest in the following spring. The foraging period coincides with the flowering of apple. Since *Osmia cornifrons* bees nest in bamboo or reed and readily accept artificial nests, beekeeping is simple for the farmer to manage with minimal skill. Presently the bees are being used as apple pollinators in more than 18,000 ha of orchards in the northern part of Japan, and furthermore the bees will be applied to other crops by shifting the adult emerging time through the control of the hibernation temperature.

The second useful insect pollinator is the European bumblebee, *Bombus terrestris*, which is a social insect. Unlike honey bees or stingless bees, the colonies are annual and only queens fertilized the previous autumn survive the winter in hibernation alone and appear in spring to start up new colonies by themselves. The first adults produced by the queen are all workers. With the progression of the season, the colony becomes more populous. Males and new queens are produced at the climax of colony development around summer. The males of the colony, whether they mated or not, die before the onset of the winter season. So do the workers. In the case of artificial nests, the colony around the climax of its development can be used for crop pollination for about 2 months. The bumble bee is considered to be an efficient pollinator of some crops because buzz-pollination of crops that require it such as Solanaceae can be achieved. Buzzing bees cling to the ends of the anthers and vibrate their indirect flight muscles, leading to pollen release.

The colonies have been imported from Europe since 1991 for pollination of tomatoes alone in glasshouses, and now more than 30,000 colonies are imported per year. These bees are popular because farmers can manage them by themselves.

The third insect is the honey bee, or the European honey bee, *Apis mellifera*. This well-known social insect is an important pollinator of orchards, fields, and large-scale glasshouses partly because of its large colony population (over 10,000 individuals), long distance flights (more than 2 km), wide range of plants on which it forages (more than 80% of cultivated crops), and availability of established beekeeping techniques. In fact, honey bees are used widely as pollinators overseas but not in Japan. Most of the Japanese farmers who need pollinators do not keep the honey bees by themselves, but, if necessary, have professional beekeepers manage the colonies. There are only 5,000 professional or semiprofessional beekeepers in Japan, the small number of which limits the use of honey bees as pollinators.

Both bumblebees and *Osmia cornifrons* bees have been commonly used mainly because the farmers can manage the bees by themselves unlike the case of honey bees. A study aimed at breeding a mutant strain of honey bees with non-stinging characteristics by using gamma radiation has been initiated so that the farmers can manage the colonies for pollination with ease[1].

Only honey bees and stingless bees are highly eusocial species living in perennial colonies which are easy to keep in hives and to be moved to any place, when necessary. As a highly eusocial bee group, stingless bees also share various useful characteristics, and could be expected to be effective crop pollinators.

Stingless bees and honey bees

Social insects show some of the following characteristics: cooperation among adults in brood care and nest construction; overlapping of at least 2 generations; and reproductive division of labor[29]. Those which display all 3 of the above characteristics are called eusocial insects. Of over 10,000 different species of social insects existing today, honey bees of the subfamily Apinae and stingless bees of the subfamily Meliponinae, have attained the most advanced social levels and they are called highly eusocial insects. The colonies of other social insects die when the fertile individual dies. But honey bees and stingless bees live in perennial colonies by replacement of the queen when needed. European honey bees and Oriental honey bees (*A. cerana*) have been kept for a long time in Europe and Asia (beekeeping or apiculture), and stingless bees have been kept in Central and South America (stingless beekeeping or meliponiculture) due to their perennial colonies.

Biology of stingless bees

The characteristics of stingless bees including *T. carbonaria* are reviewed here.

1) Distribution

Stingless bees are considered to have their center of origin in Africa and have dispersed to other tropical and subtropical parts of the world, based on paleontological and biogeographic data. This hypothesis is also supported by the fact that their primitive species with a well-developed sting system live in Africa exclusively[27)].

Stingless bees belong to the subfamily Meliponinae in the family Apidae. In general, stingless bees are easily distinguished from other bees by the following 3 characters: reduction and weakness of the wing venation; presence of the penicillum; and reduction of the sting[28)]. In contrast to Apinae which consist of only 4 main species and less than 10 species in total in the one genus *Apis*, Meliponinae are a fairly large group with diverse morphology and biology. The group contains more than 400 species. At least 250 species have been described in South and Central America where research has been most advanced. About 50 species live in South Asia and Malaysia, and 20 in Australia, Papua New Guinea, and the Philippines and as many as 40 are native to Africa. Since the forests in the tropical areas mostly consist of entomophilous plants, stingless bees are of great importance for the pollination of many wild plants in addition to tropical crops[21)].

2) Species used for stingless beekeeping

The important genera for stingless beekeeping are *Melipona* and *Trigona*. Crane listed 14 species of *Melipona* and 21 of *Trigona* that have been used in traditional beekeeping[4)]. *Melipona* species are restricted to Central and South America, and are of historical significance because of their long-time culture for the production of honey and wax. *Trigona* species are present in all the tropical continental areas, and traditional hive beekeeping with them has occurred in tropical America and occasionally in Asia. Most *Trigona* species are relatively small, and long-winged. *Melipona* species are short-winged and tend to be larger, some being as large as honey bees[4)].

T. carbonaria is very common in coastal Queensland in Australia and extends as far south as Sydney, being the southernmost species of all stingless bees in the world[16)].

3) Defense mechanisms

The stingers are vestigial and non-functional but the bees have various and efficient means of defense for colonies. Some species adopt aggressive ways of defense, like biting (*T. cupia, T. fuscipennis*), emitting a caustic liquid from the mouth (all species of *Oxytrigona*), releasing unpleasant odors (*T. capitata, M. marginata*) and irritating by crawling into eyes ears, etc. However, the most common strategy of defense is to make their nests and the entrance invisible to intruders. Therefore, most species do not harm people or animals.

T. carbonaria is a gentle species and can be manipulated with ease. The insects defend the nest by sealing up all unnecessary nest openings, and sometimes crawl over persons, and give tiny nips with their mandibles when their nest is disturbed[6)].

4) Nest structure

A few species of stingless bees build their nests in underground cavities such as termite mounds, most of them belonging to primitive groups, e.g. genera of *Meliplebeia, Plebeia*, and *Nogueirapis*. Some other species build an exposed nest which is surrounded by hard and sometimes brittle layers hanging on tree branches in the air. Those species do not seem to have ever been considered for beekeeping.

The most common type of nest is found in a tree cavity. The nest is usually made of 5 parts; brood comb, involucrum, store pots, batumen, and an entrance. The comb consists of brood cells, in each of which a single young is reared, and surrounded by a sheath of cerumen, or involucrum (Fig. 1). Therefore, the cavity where the brood cells are present is called a brood chamber. Cerumen is made of a mixture of wax secreted from the glands on the abdomen of workers and propolis, which is derived from resins collected from plants. Honey and pollen are stored in pots quite different from the brood cells. These storage pots are usually placed above and below the involucrum, and made of cerumen. The extra space in the tree cavity is sealed by batumen plates, usually made of cerumen and mud. The entrance of the nest is a simple hole. It often extends from the nest as a tube, and also continues inside the nest cavity. There are pillars and connectives inside the nest to support all the other structures within the batumen plates. The brood cells of the combs are in contact with one another, and the combs are usually horizontal, but in some species like *Trigona carbonaria*, the combs form a spiral. In subgenera, such as *Plebeia, Hypotrigona, Trigonisca, Trigona*, and *Tetragona*, some species construct cluster-type nests. This type of nest contains a cluster of brood cells irregularly arranged instead of combs. Unlike the nests with combs, cluster-type nests can take advantage of small and irregular spaces[17)].

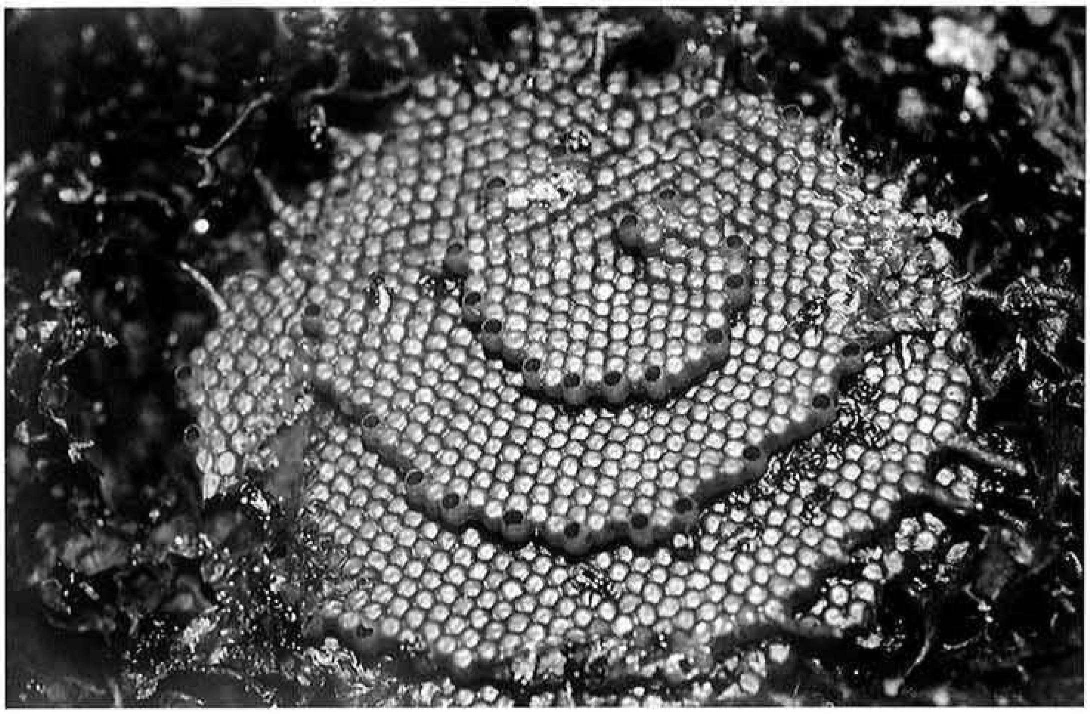

Fig. 1. Brood comb of the stingless bee, *Trigona carbonaria* showing a spiral type

Only the African species *Dactylurina staudingeri* has vertical, double combs, each consisting of 2 layers of horizontal cells opening in opposite directions, as in the case of honey bees[28].

5) Reproduction

There are 2 ways of reproduction in social insects as follows: (1) development of a colony, or increase in the number of individuals, which depends mainly on the egg-laying ability of queens. The number of eggs laid per day varies among species and does not change appreciably with the season as in the case of European honey bee subspecies; (2) colony reproduction, or increase in the number of colonies. In stingless bees, like honey bees, all the new nest foundations result from a fission of the colony. New colonies are formed by reproductive swarming with a queen and workers, but the procedure is quite different from that of honey bees[17,23]. In honey bees, an old queen leaves the mother nest when reproductive swarming occurs, but in stingless bees, young virgin queens leave, and the connection between the mother and daughter nests can last for weeks and even months. Typical formation of new colonies in stingless bees proceeds as follows: a new nesting site is searched for and identified by workers; the workers transport the necessary materials both for construction and for food from the mother nest; the new nest except for brood cells is complete; a young virgin queen flies to the new site from the mother nest along with drones; mating flights are made; and the new nest is occupied by adult bees including the new queen[17]. It has been reported that *T. julianii* and *T. varia* carry out some construction work in the new nest before the young queen arrives[18], and that stingless bees do not necessarily need to fly during mating[3]. Variations in the swarming process have been reported[11].

6) Population of nests

The number of workers comprising the colony ranges from a few hundreds to several thousands depending on the species and other factors. Wille & Michener[26] presented a list of the populations: from *Trigona corvia* 7,200 to *T. buyssoni* 136, including the major meliponiculture species: *T. schrottkyii* 300, *T. mosquito* 1,175, *T. mirandula* 2,281–4,076, *T. cupira* 2,900, *T. clavipes* 5,000–8,000, *M. marginata* 243, *M. fasciata* 200. The color of the workers is black, brown, red yellow, and white depending on the species. A mature colony of *T. carbonaria* consists of about 10,000 individuals[10].

7) Division of labor

Two kinds of division of labor can be observed in the social life of the stingless bees as in that of honey bees: division of caste referring to the reproductive system, and division of labor among workers, productive system.

The females are divided into 2 castes, queens and workers. Caste dimorphism is strongly developed. Queens are much larger than workers, lack corbiculae (the pollen-carrying structures on the hindlegs) and wax glands.

As workers age, their tasks change. Their sequence of activities can be divided into stages as follows[28]: self-grooming (just after emergence from the pupae); incubation and repairs in the brood chamber; construction and provisioning of cells, and feeding of young adults and the queen; reconstruction of the involucrum and guard duty at the entrance; and collection of pollen, nectar, and propolis. Basically the sequence of the workers' activities is similar to that in honey bees.

8) Thermoregulation

Honeybees are able to maintain the temperature around the brood at 34–36°C. The temperature is raised with their own body heat, generated by shivering the wing muscles, and lowered, if necessary, by fanning their wings at the nest entrance to draw cooler air into the nest or gathering water into the nest to spread over the comb. Generally, stingless bees are not as efficient as honey bees in controlling the nest temperature, especially when the temperature is low, they are inefficient in raising it. This may be a factor that limits stingless bees to tropical and subtropical areas. When the temperature is high, they lower the temperature by fanning their wings at the nest entrance partly for ventilation as honey bees do. Only a few species, *Trigona spinipes* and *T. duckei*, however, are known to have the ability to regulate the nest temperature within certain limits[17]. Our studies show that *T. carbonaria* can not easily control the temperature in the hive (Fig. 2).

9) Queen behavior and oviposition

The honey bee queen flies when swarming occurs, while the stingless bee queen flies only once in her life. Once she has mated and begun to lay eggs, her abdomen enlarges and she loses the ability to fly. As a result, she remains in the old nest. In contrast to honey bees, stingless bee queens are reared continuously, and tolerated in the nest for a time. Some of them establish new colonies through swarming or take over the old queen, but most are killed by workers[17].

Stingless bees provide the brood cells with the food all at once, and then close the cell just after the queen lays an egg. In the genus *Trigona*, the rearing method of queens and workers is similar to that of honey bees. Queens are reared in special large cells at the margins of the comb and filled with more larval food than workers' cells. The production of a queen depends on the amount of food during the larval stages, and any fertilized egg can become a queen or a worker, that is, growing into a queen is purely the result of a greater larval food supply, and the caste is determined trophically. In contrast, queens and workers are reared in cells with the same size and caste is determined genetically in *Melipona*. Kerr suggests that the caste genes regulate juvenile hormone production[13].

10) Foraging

The last stage of the workers' activity is foraging. Like honey bees, stingless bees collect pollen, nectar, and propolis. Most of the stingless bee species are polylectic, foraging a wide range of crops for pollen.

In contrast to honey bees, since stingless bees can forage without the help of near ultraviolet light, they can easily forage in a greenhouse with a roof made of ultraviolet-absorbing film[24]. The colonies of *T. fuscobalteata* were being kept without any problems in foraging in an environmentally controlled chamber (10 m^2, 26°C, 13L:11D with fluorescent lamps) provided properly with plant flowers[2]. *T. angustula*, *T. bipunctata*, and *T. carbonaria* can also be successfully kept in the same conditioned chamber.

11) Flight range

Stingless bees show a compact flight range compared with honey bees. The workers of honey bees can forage over 2–3 km, while those of the stingless bee can forage over 1 km at most. There are some correlations between the flight range and the body size of the workers[12]. According to Kerr[12], small bees like those of the subgenus *Plebeia* (3–4 mm) have a flight range of about 300 m, medium-sized bees, as in the case of the subgenus *Trigona* (5 mm), have a flight range of about 600 m, large bees (10 mm) have a flight range of about 800 m, and very large bees (13–15 mm), i.e. *Melipona fuliginosa*, have a flight range of about 2,000 m[28]. Flight activity of stingless bees is constantly influenced by the weather conditions[8]. In *M. marginata*, the flight activity is correlated positively with the temperature and negatively with RH, but the behavior indicates a flexible response to prevailing weather conditions[14]. In *T. carbonaria*, foraging bees fly over a maximum distance of 500 m and usually prefer to fly over a distance of about 100 m from the nest[10].

12) Communication

Like the honey bees, many species of stingless bees are able to communicate the location of a food source. They use a chemical secreted from the mandibular gland and sunlight for orienteering. Foraging workers stop at intervals of a certain distance and leave scented spots on the way from a good source of food to the colony. Other bees leave the nest and begin to follow the odor trail outward[28]. In *Trigona postica*, the foraging workers seem to be able to act as guide bees by leading the others in a group back and forth for several trips[5]. Some species of stingless bees such as *T. angustula* communicate with sounds and zigzag running. In *M. quadrifasciata* and *M. merillae*, returning foragers produce sound impulses varying proportionally to the distance of the food source[7]. In *T. carbonaria*, a foraging bee that has located a good food source marks it with a chemical scent to help other workers find it.

13) Longevity of colonies

The colony of stingless bees could last permanently by replacing the queen successively as long as a lethal disaster does not occur. Generally, the longevity of the queens seems to be longer than that of the honey bees which is 3–5 years[28]. We obtained a colony of *T. fuscovartiata* from Thailand in 1995, when the colony was 12 years old. We have kept it under environmentally closed conditions for more than 3 years since then. It is still in good condition and there has not been any exchange of queen. The workers of stingless bees also seem to live considerably longer than those of honey bees. For instance, *T. xanthotricha* workers spend about 6 weeks in the nest and then about the same length of time in the field, a lifespan about double of that of a honey bee[20].

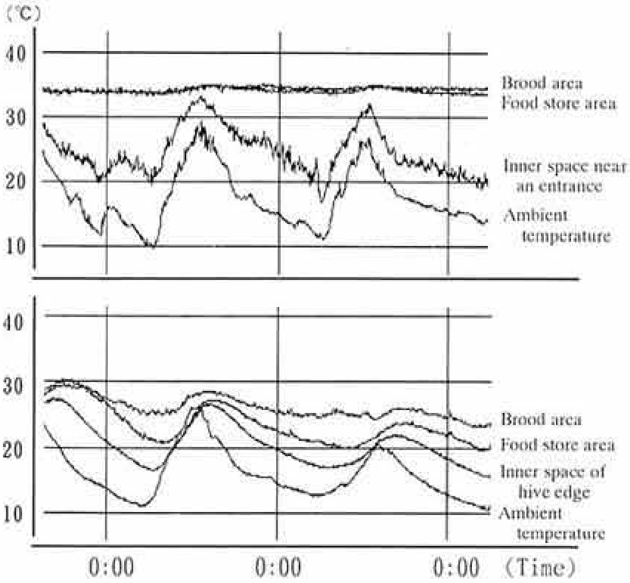

Fig. 2. Temperatures in and out of the nest of the honeybee, *Apis mellifera* (above), and the stingless bee, *Trigona carbonaria* (below)

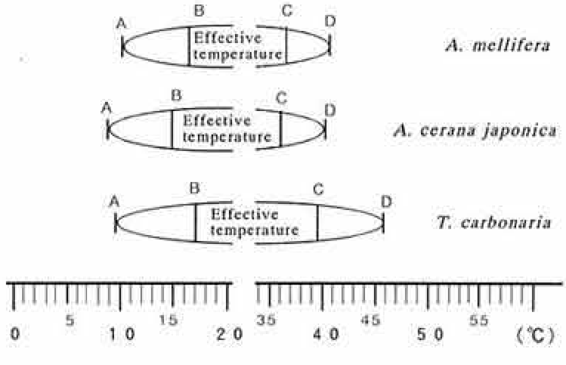

Fig. 3. Thermo-responses of adult workers in 3 species
A: Lethal low temperature.
B: Effective low temperature.
C: Effective high temperature.
D: Lethal high temperature.

14) Pollination efficiency

Although few quantitative data are available on the influence of pollination by stingless bees on crop yield, many species are considered to be useful for pollination of plants[9], although some species can not be used. *T. silvestriana, T. fulviventrid* and *T. textacea* damage the corolla of *Thunbergia grandiflora*[30].

T. carbonaria is polylectic and an effective potential pollinator of crops such as the nut-bearing tree, *Macadamia integrifolia*, and also quickly adapts to new plants previously unknown[10,25]. In fact the foraging bees thrive

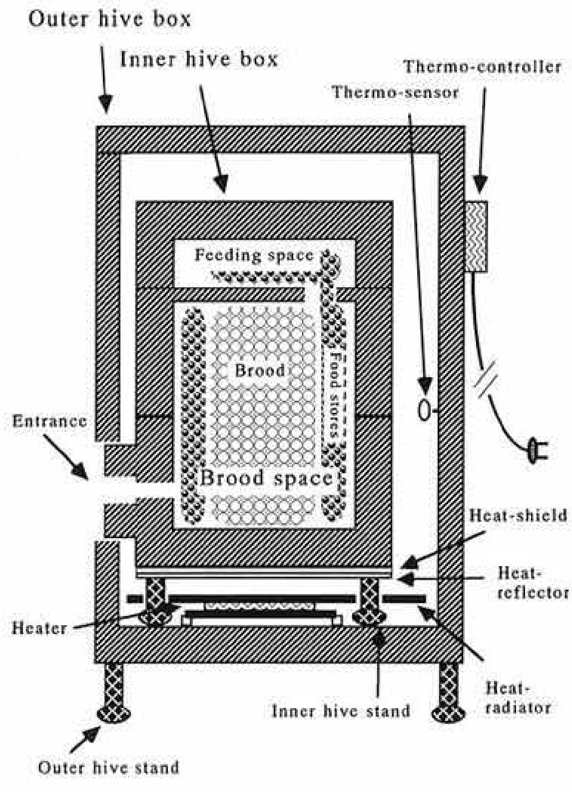

Fig. 4. Thermo-controlled hive box for the stingless bee, *Trigona carbonaria*

on a wide variety of Japanese flowering plants they have never seen before, which we provided in our experiment. Two hives per 10 a of crop fields would be recommended for sufficient pollination[10].

Stingless beekeeping

Before honey bees were imported to South and Central America, stingless bees were the only honey producers in these areas. Even presently hives of stingless bees are kept for honey harvest, and some researchers have outlined in detail the management and domestication of several stingless bee species. Various kinds of hives have been designed according to the species to facilitate honey harvesting and avoid the destruction of the nest[19].

1) Hives for T. carbonaria

Researchers in Australia have developed various types of hives for *T. carbonaria*[6]. As shown in Fig. 2, *T. carbonaria* are not able to control the temperature in the hive, compared with honey bees. The tolerance of low temperature in *T. carbonaria* adult bees is not appreciably different from that in the honey bees (Fig. 3). The honey bees form a cluster when the ambient temperature is fairly low, as the temperature in the hive remains within the optimum range, unlike *T. carbonaria*. Therefore, the major problem for keeping them in Japan is how to maintain them safely under warm conditions. We have tried to design a hive in reference to Heard's works, so as to make the bees survive throughout the year and even enable them to multiply the colony in Japan. The hive consists of two boxes, an inner hive box and an outer box (Fig. 4). The inner box is designed with three stories to contain a brood space, food storage space, and feeding space. The brood space can be divided for propagating the colony. The outer box is equipped with a heater system which keeps the hive at a fixed temperature even in the winter season.

2) Splitting the colony

To multiply the colony, the nest, especially brood, should be split. The layers of *T. carbonaria*'s brood cells form a single spiral, that is, a single comb. The summit and the advancing edges of the spiral comb are a growing portion where new cells are constructed and added along them. When the summit reaches the ceiling of the brood chamber, the growing portion appears again at the bottom to repeat its rise[16]. To split a nest, the inner box is prized open while the brood in a brood space is cut in half. New empty inner boxes are then added to each half of the original inner box. Then 2 new nests are formed. There is no problem with the new nests which contain the original queen. Consequently the other one does not contain queens. However, in this species, usually several large cells contain developing queen bees, scattered throughout the brood comb. One of these cells will grow to become a queen[6].

By using this type of hive boxes, we have succeeded in keeping the colonies of *T. carbonaria* in Japan with a view to using them as pollinators of crops in glasshouses.

References

1) Amano, K. (1997): Successful breeding of non-stinging honeybees. *Farming Jpn.*, **31** (5), 36–42.
2) Amano, K & Boongird, S. (1997): Keeping of the stingless bee, *Trigona fuscobalteata* (Hymenoptera: Apidae) in an environmentally enclosed chamber. *Annu. Rept. Prot. North Jpn.*, **48**, 210–212 [In Japanese with English summary].
3) Camargo, C. A. (1972): Mating of the social bee *Melipona quadrifasciata* under controlled conditions. *J. Kans. Entomol. Soc.*, **45**, 520–523.
4) Crane, E. (1992): The past and present status of beekeeping with stingless bees. *Bee World*, **73**, 29–42.
5) Cruz-Landim, C. et al. (1968): Mandibular gland development and communication in field bees of *Trigona (Scaptotrigona) postica*. *J. Kans. Entomol. Soc.*, **41**, 474–481.
6) Dollin, A. & Heard, T. (1998): Keeping Australian stingless bees in a log or box. *In* Native Bees of Australia Series Booklet 5. Australian Native Bee Research Center, 1–14.
7) Esch, H. et al. (1965): Sound; an element common to communication of stingless bees and to dances of the honeybee. *Science*, **149**, 320–321.
8) Heard, T. A. et al. (1993) Factors influencing flight activity of colonies of the stingless bee *Trigona carbonaria* (Hymenoptera: Apidae). *Aust. J. Zool.*, **41**, 343–353.
9) Heard, T. A. (1999): The role of stingless bees (Meliponinae) in crop pollination. *Annu. Rev. Entomol.*, **44**, 183–206.
10) Heard, T. A. & Dollin, A. (1998): Crop pollination with Australian stingless bees. *In* Native Bees of Australia Series Booklet 6. Australian Native Bee Research Centre, 2–17.
11) Imperatriz-Fonseca, V. L. (1975): On swarming activity in Meliponinae. *In* Proc. 25th Int. Apic. Congr., 298.
12) Kerr, W. E. (1959): Bionomy of Meliponids. VI. Aspects of food gathering and processing in some stingless bees. *In* Food gathering in Hymenoptera. Symp. Entomol. Soc. Am. Detroit, 24–31.
13) Kerr, W. E. (1974): Sex determination in bees. III. Caste determination and genetic control in *Melipona*. *Insectes Soc.*, **21**, 357–367.
14) Kleinert-Giovannini, A. et al. (1987): Aspects of the trophic niche of *Melipona marginata marginata* Lepeletier (Apidae, Meliponinae). *Apidologie*, **18**, 69–100.
15) Maeta, Y. et al. (1992): Utilization of the Brazilian stingless bee, *Nannotrigona testaceicornis* as a pollinator of strawberries. *Honeybee Sci.*, **13**, 71–78 [In Japanese with

English summary].

16) Michener, C. D. (1961): Observations on the nests and behavior of *Trigona* in Australia and New Guinea. *Am. Mus. Novit.* **2026**, 1–46.

17) Michener, C. D. (1974): The social behavior of the bees; A comparative study. Cambridge, Mass, Harvard Univ. Press, pp. 404.

18) Moritz, R. F. A. (1986): Genetics of bees other than *Apis mellifera*. *In* Bee genetics and breeding. Academic press Inc., 121–154.

19) Nogueira-Neto, P. (1951): Stingless bees and their study. *Bee World*, **30** (10), 73–76.

20) O' Toole, C. & Raw, A. (1991): Bees of the world. Blandford (a Cassell imprint), London, pp. 192.

21) Roubik, D. W. (1990): Biogeographical ecology of *Melipona* (Apidae: Meliponinae). *In* Proc. 11th Int. Congr. IUSSI, 379–380.

22) Sakagami, S. F. (1957, 58): Biology of the stingless bee and its domestication (1), (2). *Seitai-kontyu*, **6** (15), 101–116, **7**(1), 28–46 [In Japanese].

23) Sakagami, S. F. (1982): Stingless bees. *In* Social insects. Vol 3. ed. Hermann, H. R., Academic Press, New York, USA, 362–376.

24) Tezuka, T. & Maeta, Y. (1993): Effect of UVA film on extranidal activities of three species of bees. *Jpn. J. Appl. Entomol. Zool.*, **37**, 175–180.

25) Wallace, H. M., Vithanage, V. & Exley E. M. (1996): The effect of supplementary pollination on nut set of *Macadamia* (Proteaceae). *Annu. Bot.*, **78**, 765–773.

26) Wille, A. & Michener, C. D. (1973): The nest architecture of the stingless bees with special reference to those of Costa Rica. *Rev. Biol. Trop.*, **21**, Suppl. 1, pp. 278.

27) Wille, A. (1979): Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. *Revista de Biologia Tropical*, **27** (2), 241–277.

28) Wille, A. (1983): Biology of the stingless bees. *Ann. Rev. Entomol.*, **28**, 41–64.

29) Wilson, E. O. (1971): The insect societies. Belknap Press of Harvard University Press, Cambridge, Mass., pp. 548.

30) Young, A. M. (1983): Nectar and pollen robbing of *Thunbergia grandiflora* by *Trigona* bees in Costa Rica. *Biotropica*, **15** (1), 78–80.