

DIVERSITY OF STINGLESS BEES AND HOST PLANTS IN THONG PHA PHUM DISTRICT, KANCHANABURI PROVINCE

INTRODUCTION

Tropical forests are the world's richest and most productive ecosystems, containing half of all living species on the planet (Wilson, 1988). In addition to diversity, the forests are a deterrent against the greenhouse effect, and they contain a genetically rich resource—a yet virtually untapped wealth of plants whose curative properties could benefit humankind. Tropical forests comprise some of the most complex and diverse ecosystems on the planet.

The nature of land-use change in recent decades has not only resulted in a dramatic decrease in total forest cover, but also in an increasingly skewed size-distribution. Both of these changes contribute to the present-day concern over the loss of biodiversity and species extinction rates. In addition, some recent studies have shown that the diversity and abundance of several animal taxa in agricultural landscapes decline significantly with increasing distance from native habitats. Of all the taxa shared by native and agricultural habitats, pollinators are among the most ecologically important and of greatest concern in conservation.

Pollination is one of the most critical reproductive processes in plants, and in tropical forests it is mostly mediated by animals. One-third of the human diet in tropical countries is derived from insect-pollinated plants, so the worldwide decline of pollinators has potential consequences for the stability of crop yields. The bee fauna of the Oriental region is the poorest (89 genera) in the world (Michener, 1979) and, accordingly, the bee fauna in tropical South-east Asia is also species poor, despite extremely high plant species richness (Whitmore, 1984). However, tropical bee communities are more ecologically diverse (Roubik, 1992). This means that each species potentially pollinates more plants species and may have a greater part in

maintaining fertilization and genetic diversity in angiosperms than bees in other regions.

South-east Asia is well-known for its diversity of social bees, even though the general bee fauna in tropical South-east Asia is rather poor in species compared with the Neotropical region and tropical Africa (although this region has a rich angiosperm flora). This may be related to humid weather conditions throughout the year, since bees are most diverse in the warm temperature dry regions. South-east Asia is full of bees, albeit with fewer species. In the tropical rainforest of South-east Asia, most tree species in the canopy stratum bloom at irregular intervals of one to four years (over periods of three to four months), during what is called “general flowering”. Social bees, such as honeybees and stingless bees are the most important pollinators in these forests in terms of the numbers of plant species pollinated. Stingless bees were observed to pollinate 61 out of 280 (22.6%) plant species in a lowland mixed dipterocarp forest in South-east Asia. Several countries have recently developed initiatives to conserve and protect pollinators, which are declining in many parts of the world. Fragmentation-induced changes in the structure of the pollinator guild may have far-reaching consequence for gene flow in plant population and for plants and animal community dynamics. Studies of tropical forest systems have made important contributions to understanding patterns of species diversity and community structure. Due to increasing global habitat destruction modern studies of diversity are of vital importance for understanding biological communities and their conservation.

Highly social honey bees and stingless bees are the predominant group of flower-visiting insects and likely pollinators in the Old and New World tropical forests. Stingless bees (Apidae, Meliponini) play an important role in the pollination process of plant life, particularly wild flower in most tropical countries. Stingless bees live socially in perennial colonies of a few hundred up to several thousands of individuals (Wille, 1983). Stingless bees are generalists and visit many different flower types. Rather than being highly specialized flower visitors they are generally polylectic and forage on an array of food plants that provide some pollen and nectar over much of the year. On the population level some species are known to use floral

resources from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms *et al.*, 1996). Niche overlap between different stingless bee species was frequently found to be high in studies of flower visitation, although some selectivity has been reported, at least on the sub-tribal level (Heithaus, 1979; Ramalho, 1990; Wilms *et al.*, 1996).

Human activities, such as commercial logging and non-traditional shifting cultivation, have caused rapid changes in tropical forest. In Thailand, large areas of natural forest remain, although changes in land use, such as the establishment of oil palm plantations, are increasing. In addition, selective logging has disturbed most of the remaining natural forest. These human disturbances not only directly affect the community structure of forest trees but may also indirectly influence the pollinator community. This indirect effect is probably quite strong with respect to stingless bee, because they depend on forest tree for both food (nectar and pollen) and habitat (nest site). Although decreases in the species richness and population density of stingless bees seems to be proportional to the intensity of human disturbance, the mechanisms responsible for these declines in the stingless bee community are still unclear. To date only one study has directly addressed ecological factors that are potentially limiting to stingless bee populations.

In spite of the importance of stingless bees as potential pollinators in both agricultural and natural ecosystems and the distinctive quality of their honey, there is limited information on food sources that stingless bees utilize for nectar and pollen. Analysis of the pollen spectrum of the pollen load can indicate the plants visited by stingless bees and permits the characterization of bee plants in a geographic region or at a time of the year.

The present study investigates the factors that limit stingless bee populations by measuring nest density, species diversity and pollen usage in four types of forests. External pollen sources are a likely supplement to the bee diets at times when little flowering occurs inside the forest, thus increasing overall stingless bee carrying-capacity.

Species diversity is a parameter of community structure involving species richness and their abundance for the taxa (Wang *et al.*, 2000). In general, species diversity and complexity of association among species are essential to the stability of the community. Basic information about species richness and abundance of stingless bees is required for future taxonomic work on stingless bee in South-east Asia.

This is the first study of the biodiversity of stingless bees in western Thailand. The study site was representative of forests in Thailand because it had four important types of forest (dry dipterocarp forest, upper mixed deciduous forest, lower mixed deciduous forest and dry evergreen forest). This study is the first time the diversity, nest density and host plants of a large community of stingless bees have been studied simultaneously in Thailand.

To my knowledge there has been no study so far that has linked pollen foraging and resource partitioning to floral resource availability in the habitat. The analysis of forager pollen loads has proven to be a useful tool in assessing bee diet as it is independent of flower accessibility and allows for equally high resolution in the forest canopy and understory. The food resources that stingless bees visit and use have been relatively well studied. However, little is known about their preference for trees to nest in

Stingless bees are distributed over the country and form an important group of pollinators in agricultural and natural ecosystems. However, hardly any information exists on the biology and ecology of the stingless bees in Thailand. For this reason I studied the characteristics of stingless bee species that are common in four types of forest in Thong Pha Phum District, Kanchanaburi Province.

These studies are directly relevant to ecological factors and habitats that are important in the Kanchanaburi Province. However, hopefully they will offer new insight to the ecology of bees in terms of elevation and land use - insights that can be applied more globally to conserve and develop native bees as agriculture pollinators.

In addition, these results will create baseline data on Thailand's bees that can be used to monitor populations in the future.

The information obtained is a first step towards a better conception of the use of trees by stingless bees and will help to analyze the effects of alternations in the composition of vegetation on bee populations. By this means, biodiversity restoration programs can be improved. The information acquired forms valuable building blocks for the development of an integrated pollination management program in Thailand.

Therefore, this study attempts to clarify the species of stingless bee and host plants of stingless bee in order to give guidelines for both conservation strategies and for operational techniques for managing indigenous, stingless bee colonies.

OBJECTIVES

1. Taxonomic study of stingless bees in the four types of forest of Thong Pha Phum District, Kanchanaburi Province, Thailand.
2. To investigate the species diversity of the stingless bee fauna in the four types of forest of Thong Pha Phum District, Kanchanaburi Province, Thailand.
3. To observe the species richness and abundance of stingless bees in the four types of forest of Thong Pha Phum District, Kanchanaburi Province, Thailand.
4. To test whether vegetation structure and microclimate are correlated with the distribution of stingless bee species in the four types of forest.
5. To identify the plants that are visited by stingless bees in the four types of forest.

LITERATURE REVIEW

Stingless bees have populated tropical earth for over 65 million years-longer than honey bees (Camargo and Pedro, 1992; Michener, 2000). Stingless bees probably arose as a pivotal force in the ecology of tropical forests at the end of the Cretaceous period (Michener and Grimaldi, 1988), their emerging influence being based on their diversity and local abundance.

Stingless bees are a group of small-to medium-sized bees, with a vestigial sting. In terms of numbers of species, they are a large group of bees, comprising the subfamily Meliponinae (tribe Meliponini, sometimes called stingless honey bees) in the family Apidae. Taxonomically, they are most closely related to the common honey bees (Apini), carpenter bees (Xylocopini), orchid bees (Euglossinae) and bumblebees (Bombinae). The common name is slightly misleading, as a great many other bee species, especially in the family Andrenidae, are also incapable of stinging.

1. Taxonomic status

Stingless bees are often known as Thai native honey bees. They are also known as native bees, sugar bag bees and sweat bees. The bees are small in size and, as the name implies, do not sting.

The valves of the sting of stingless bee are reduced to blunt structures which cannot be protruded, and also they can not be used as piercing organs. Instead, stingless bees use their mandibles to defend themselves. The Thai name “channarong” is derived from the habit of collecting resin (“chan” in Thai) for nest building. Stingless bees have different names in each region of Thailand according to the behavior encountered. For example, in the northeastern region, stingless bees are called “keetungnee” or “keesood” which refers to the collecting of resin, the swarming habit and the never-let-go biting of enemies. People in the north and the east call them “toong-ting” from the appearance of the hind legs which hang vertically when the bees are flying (Anonymous, 2006).

The estimated, several hundred species of stingless bees worldwide are arranged into 21 genera. The most important genera are *Melipona* and *Trigona*. *Melipona* consists of about 50 species and is confined to the Neotropical region. *Trigona* is the largest genus and is the most widely distributed with about 130 species (Heard, 1999).

Scientific classification

Class: Insecta

Order: Hymenoptera

Superfamily: Apoidea

Family: Apidae

Subfamily: Apinae

Tribe: Meliponini

2. General morphology

As noted above stingless bees belong to the subfamily Apinae, one of the three subfamilies of the family Apidae. In general, they are easily distinguished from other bees by the following three characters:

- Reduction and weakness of the wing venation.

- Presence of the penicillum, a brush of long, stiff setae located anteriorly on the outer apical margin of the hind tibia. This structure is unique to the Meliponinae; it is absent or much reduced and soft, however, in the subgenus *Hypotrigona* and the parasitic genera *Lestrimelitta* and *Cleptotrigona*.

- Reduction of the sting.

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 body of a stingless bee (Figure 1) varies from trigoniform to apiform in general appearance, is sparsely hairy, short-haired or moderately hairy, and 3-15 mm in length. Body colors range from black, to reddish, to brown and some species have conspicuous yellow or cream markings.

The males of stingless bees have eyes that are much larger than those of the females and their ocelli are almost in a straight line on the vertex rather than forming the usual triangle. The malar space (i.e. that part of the head capsule between the compound eye and the base of the mandible) is large in workers and queen but very narrow in male. The antennae are geniculate in both sexes, and are 13-jointed in males, and 12-jointed in females. The mouthparts are of the chewing-lapping type. The labial glossa forms a hairy tongue. The mandibles vary from dentate to almost spoon shaped. In general, the mouthparts tend to be shorter in queens and males than in workers (Michener, 2000).

The wings are long and ample. In the forewing as the usual hymenopteran nervures are very incomplete. The stigma is well marked and the radial cell (= 3R1) is elongate, reaching to the apex of the wing. However, the cubital and discoidal cells (= 1Rs, 2Rs, 1M, 2M, etc.) are often opened apically, or at least the distal parts of their veins are much narrower than their basal parts near the stigma.

Legs: All three pair of legs are well developed. The posterior (hind) tibia is flattened and very broad. The legs of workers are fringed with hair above and below, forming a corbicula or pollen-basket. In the male, the posterior tibia and tarsi are more rounded.

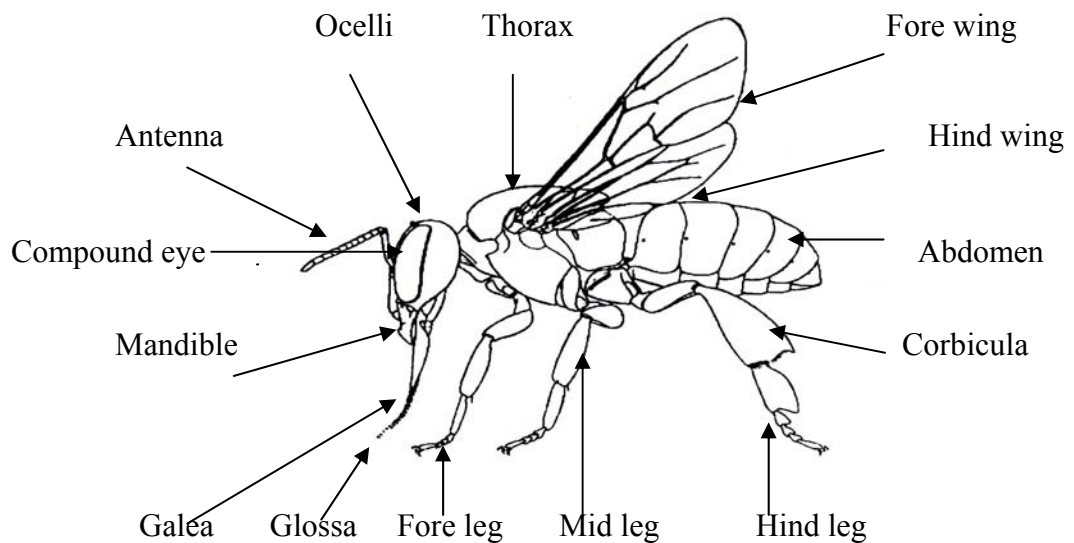


Figure 1 The external morphology worker of a stingless bee.

Source: modified from Francisco (2004)

3. Biology of stingless bees

Stingless bees belong to one of the most primitive types of highly eusocial bees in the world and they have some basic features in common with honey bees. Like honey bees, stingless bees live socially in perennial colonies ranging from a few hundred bees to several thousands of individuals, normally all descendants of a single queen (Michener, 1974; Sakagami, 1982). Typically stingless bees are tropical or subtropical, eusocial, with perennial colonies and about 6,000 adult bees per nest (Roubik, 1992). The adult population of a stingless bee nest is composed of queen, drones and workers.

The queen: The determination of caste is different in the two genus of the subfamily Meliponinae. In the genus *Trigona* the most important factor is the quantity of food received by a larva during its development.

Stingless bees provide the brood cells with the food required to produce a new bee all at once, and then close the cell just after the queen lays an egg. In the genus

Torigona, the rearing method of queen and worker is similar to that of honey bees (Michener, 1974).

Queens develop in special large cells at the margin of the comb; these cells are filled with more larval food than workers' cells (Sakagami, 1982). 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. Thus, growing into a queen is purely the result of a greater larval food supply, and the caste is determined trophically. However, this is not always the case in stingless bees. In the genus *Melipona* (Meliponini) the queen cells are of the same size as those of workers and males. In this genus, the determination of caste is influenced by both nutritional and genetic factors. The individuals that have genetic potential to become a queen will do so only if they receive an adequate quantity of food. Kerr (1974) suggests that the caste genes regulate juvenile hormone production.

Queens are much larger than workers, and lack of wax glands, and corbiculae (the pollen-carrying structures on the hind legs). The queen is a fertile female and this is the only bee in the nest that can lay fertile eggs and control the population in the nest. After mating, her abdomen becomes so large and swollen with eggs that she cannot fly. The queen never leaves the nest. She spends most of her time in the brood chamber and is a central figure in the life of the nest (Michener, 1974).

If other queens develop in a colony that already has a mated queen and it is not the swarming period, these queens will either be killed or abandon the colony. In *Tetragonisca angustula*, *Plebeia* spp., *Friesella schrottkyi*, *Frieseomelitta varia* and *Schwarziana quadripunctata*; there are special cells for the imprisonment of the queen. These are chambers built with cerumen where virgin queens are kept and fed for some time. In *Melipona* and some species of Trigonini, such as *Scaptotrigona postica*, there are no special cells for the imprisonment of virgin queens (Roubik, 2006).

The drones: The male bees of the nest are called drones. All male stingless bees are fertile. Their main role in their life is mating with a new virgin queen. They have very large eyes and long antennae. Since they do not collect honey or pollen for the nest, they do not have specially-shaped legs as do the workers. Occasionally large swarms of drones are seen outside the nests of stingless bees. These may be mating swarms.

In stingless bees, as in the other Hymenoptera, the males are born from non-fertilized eggs and are thus haploid. When the colonies attain a large population the males are produced in great numbers as well as queens. In many species, the majority of the males are produced via oviposition by workers (John *et al.*, 1999).

The workers: There are hundreds or even thousands of sterile female bees in each nest. They perform different tasks at different stages of their lives. After they hatch, they care for the immature bees in the brood, perform self-grooming (just after emergence from the pupae), produce wax and work in the brood nest. Later they help guard the nest entrance. Then, in the last weeks or so of their lives, they busy themselves with incubation and repairs in the brood chamber, construction and provisioning of cells, feeding of young adults and the queen, cleaning of the nest, reconstruction of the involucre, foraging on flowers for collection of pollen, nectar, propolis and other materials, and reception and ripening of nectar. They build wax structures like honey pots at various times throughout their lives (Wille, 1983). Basically the sequence of the workers' activities is similar to that in the honey bees.

There are two ways of “reproduction” in social insects:

- 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. The process of swarming in stingless bees is rather different from the one found in *Apis mellifera*. The honey bee queen flies when swarming occurs (which may happen on more than one occasion), 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.

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. 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:

1) Some workers fly in search of a place for the new nest.

2) When the workers find a suitable place, they begin the construction of the new nest, using material from the mother colony. The workers transport the necessary materials both for construction and for food from the mother nest. The new nest is complete, except for brood cells, only after the bees have built the nest entrance, pots and involucrum.

3) Only after the new nest has been provisioned, does the virgin queen leave the old colony and fly to the new site from the mother nest along with drones.

4) The new queen makes her nuptial flight, where she is mated by only one male. The new queen assumes control of the new nest which initially is occupied only by adult bees. The queen's ovaries initiate egg development, enlarging the abdomen

so that she cannot fly anymore. Some days later, she begins laying eggs. Return visits of some workers to the mother colony may go on for a long time, even after the complete establishment of the new colony.

It has been also reported that *Trigona julianii* and *T. varia* workers carry out some construction work in the new nest before the young queen arrives (Moritz, 1986), and that stingless bees do not necessarily need to fly during mating (Camargo, 1972).

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 and Michener (1973) presented a list of the population sizes for a number of species: from *Torigona corvia* with 7,200 individuals to *Trigona buyssoni* with only 136. Population sizes are quite variable across the major meliponiculture species: *T. schrotkyii* 300, *T. mosquito* 1,175, *T. mirandula* 2,281-4,076, *T. cupira* 2,900, *T. clavipes* 5,000-8,000, *Melipona marginata* 243 and *M. fasciata* 200. A mature colony of *T. carbonaria* consists of about 10,000 individuals (Heard and Dollin, 1998).

Life cycle

Sakagami *et al.* (1989) studied the biology of *Trigona moorei* and found that the life cycle of these bees lasts 36-38 days. Pobsuk (2006) also studied the biology of *T. apicalis*, *T. collina* and *T. pagdeni* in Kanchanaburi Province, Thailand. Life cycle of those bees from egg to adults lasted 35, 39 and 48 days respectively. Stingless bees undergo complete metamorphosis starting from egg, larva, pupa and adult. The eggs are oblong and translucent and stick to the surface of the food mass in the cell tube. After 7 days, the larvae hatch from the eggs and commence feeding on the food mass of mixed pollens and honey. There are 5 instars and the larval stage lasts 38-42 days. The pupal stage ranges from 22-27 days. The newly emerging adults are referred to as “callow”. They have the typical form and size of stingless bees but are light brown in

body color caused by incomplete melanization. After the callow stage, the color becomes darker (first at the front of the body and then progressively towards the back), until the appearance of the full grown adult is reached.

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 greater than that of honey bee queens which is 3-5 years (Wille, 1983). Amano and Boongird (1997) obtained a colony of *Trigona fuscovariata* from Thailand in 1995, when the colony was 12 years old, and 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 the 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 that of a honey bee worker (O' Toole and Raw, 1991).

4. Nest structure

Because nests are notable points of bee activity and often spectacular samples of animal architecture, nesting biology is a highly visible aspect of stingless bee behavior (Michener, 1974).

Stingless bees, in a general way, build nests that are more complex nests than the nests of honey bees (*Apis mellifera*, *A. cerana* and *A. florea*). They exhibit a great variety of forms, size and place of construction.

The nest is usually made of five parts (an entrance, storage pots, brood comb, involucre and batumen) (Figure 2). Nests of most stingless bees are mainly constructed with cerumen. Cerumen is made of wax secreted from the glands on the

abdomen of workers mixed with resins and gums (propolis) collected from plants and brought to the nest (Sakagami, 1982; Wille, 1983).

In all cases the central brood and storage area is enclosed within a layer of cerumen, except for the entrance hole (Sakagami, 1982; Sakagami *et al.* 1983; Sakagami and Yamane, 1984). Within this envelope brood cells are constructed in clusters or combs.

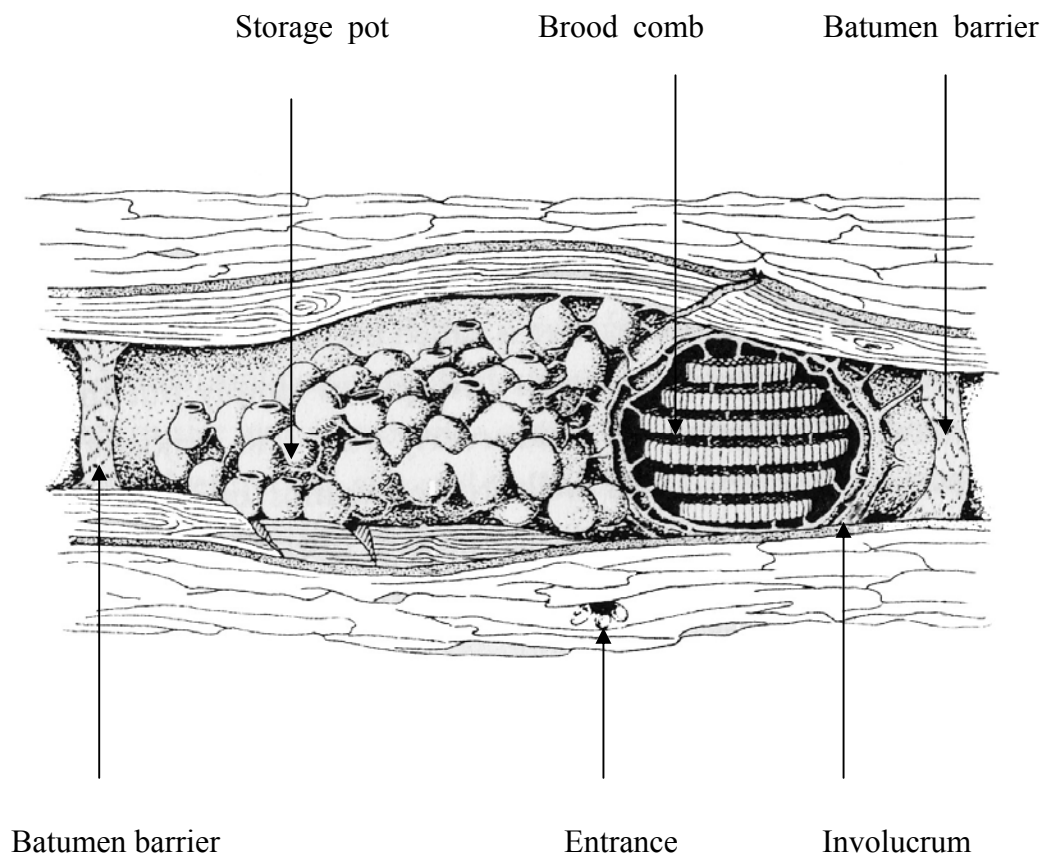


Figure 2 Diagram of stingless bee nest.

Source: modified from Weiss (2002)

The entrance: 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. Individual variation in architecture, for instance elaboration of the nest entrance or thickness of resin enclosing the internal nest, likely relates to (1) nest age, (2) bee genetics and (3) micro-environment, including predators, parasites, symbionts, rain, wind and sun (Wille, 1983; Sakagami *et al.*, 1983b; Melo, 1996).

The entrance to a stingless bee nest is normally built of wax and mud. The form of the entrance varies greatly from one species to another and it is useful in the orientation of the bees and for the defense of the nest.

After the entrance, there is a passageway, generally built of propolis, ending in the storage pots. In the genus *Partamona*, between the entrance and the nest itself there is a structure called the vestibule that is similar to the nest and disorients parasites and predators, sometimes acting as an effective defense device (Camargo and Pedro, 2003).

The storage pots: Between the entrances itself and the storage pots, generally there is a covered way made from propolis.

The colony's food resources are stored in separate "pots" (pollen pots and honey pots). Stored nectar or ripened honey are generally in nest cavity extremes (especially for storage during heavy flowering periods), while pollen and some honey surround the brood area. However, robber bee genera *Lestrimelitta* and *Cleptotrigona* collect and then store some mixed honey and brood provisions (Sakagami *et al.*, 1993).

The storage pots are made with cerumen and normally have a spherical to ovoid shape. The food storage containers are small to large spheres, or are egg-shaped, or even conical or cylindrical. Often pots are pressed together in odd conglomerates, as are the brood cells, ranging from individual cells on pillars, to sheets of orderly cells on combs, separated by the pillars.

The pollen pots are longer and larger than the honey pots. Some species such as *Frieseomelitta varia* build honey pots that are different from the pollen pots. The latter are longer and larger than the honey pots which have an oval shape (Roubkik, 1983). The brood comb can be horizontal (in the subfamily Meliponinae, only *Dactylurina staudinger*, an African species, has vertical combs as those in *Apis mellifera*) or in a cluster in which the brood cells lack common walls. The latter kind of brood cell arrangement can be found in *Frieseomelitta varia*, *F. silvestrii* and others.

The amount of honey stored in the colony varies enormously among the species, with some such as *Melipona scutellaris* and *M. compressipes* storing more than 8 litres during a year, and others like *Plebeia* spp. storing only a few cubic centimeters (Veen and Sommeijer, 2000).

The involucre: The brood combs, and sometimes the storage pots, are in many species (such as *Frieseomellita varia* and *Frieseomellita silvestrii*) enveloped by a series of membranes of cerumen which is called the involucre. This is important for thermoregulation of the nest. Some species, such as *Leurotrigona muelleri* and *Trigonisca* spp., use pure wax. The bees that build exposed nests (such as *Trigona spinipes*) use leaves and other vegetation parts mixed with resin. *Partamona cupira* workers use mud and sometimes faeces in the construction of their semi-exposed nests.

The brood comb: The brood combs are made of cerumen, and are suspended and separated by connectives and pillars. *Partamona cupira* has permanent pillars that pass completely through the brood area and are made of mud resin and wax. The species that construct nests in underground cavities isolate the nest using a series of membranes of batumen constituted of resin, mud and wax. Exposed nests also have a involucre constituted of resin and other vegetation parts (such as in *Trigona spinipes*) or resin and mud (as in *P. cupira*).

In the construction of the brood comb each cell is fully built and provisioned before oviposition by the queen. The comb consists of brood cells, in each of which a single young is reared, surrounded by a sheath of cerumen or involucre. Therefore, the cavity where the brood cells are present is called a brood chamber. The number of eggs laid per day varies considerably within a species and from one species to another according to the situation of the colony, especially in relation to the food available. The number of cells produced per day varies from 10 in *Melipona* colonies up to several hundred in *Trigona* species (Sakagami, 1982). After oviposition the workers close the cell and have no contact with the new bee until it emerges. If the immature bee dies or the food store spoils (e.g. as result of excessive temperatures) then the workers may tear open and clean out the closed cells.

After the larva finishes feeding, it makes a silk cocoon, and the workers gnaw away the cerumen of the cell. That is the reason why new brood combs have the color of cerumen and are fragile, while the older combs, where the larvae have already spun cocoons, are clearer in the upper part and are more resilient.

The combs are usually horizontal and they have a concentric growth. But in *Trigona carbonaria* the combs form a spiral. Only in *Dactylurina* are the combs vertical and double layered, with the horizontal cells of each comb opening in opposite directions, which is a remarkable parallel to the cell arrangement used by honey bees (Nogueira-Neto, 1997).

In subgenera, such as *Plebeia*, *Hypotorigona*, *Trigonisca*, *Torigona*, and *Tetragona*, some species construct cluster-type nests. This type of nest contains a cluster of brood cells arranged irregularly instead of in combs.

Some *Plebeia* build the regular pancake-like stack of brood cells separated by pillars and arranged in circular combs, like that made by most other stingless bees, whereas the smallest species do not build combs but instead make loose chains of cells or clusters. *Austroplebeia* build loose combs, which is perhaps an intermediate comb condition (Michener, 1961).

Unlike the nests with combs, cluster-type nests can take advantage of small and irregular spaces (Michener, 1974).

The extra space in the tree cavity of the typical stingless bee nest is sealed by batumen plates, usually made of cerumen and other materials like mud.

Sakagami *et al.* (1989) studied the Malesian stingless bee, *Trigona (Trigonella) moorei* Schwarz, which is obligatorily myrmecophilous. All 67 nests collected in Indonesia, were found within active, arboreal, carton nests of *Crematogaster* ants. Nest architecture for this stingless bee is characterized by a slender, sticky entrance tube, brood cells arranged as separate, U-shaped horizontal combs, queen cells that often form a cluster isolated from combs, and a brood area encircled with pillars or thin, single-layered involucrum.

Type of nest (nest sites)

Species vary greatly in their choice of nest site. Sites range from exposed nests constructed in vegetation to subterranean nests in underground cavities and nests in pre-existing cavities in trees (Darchen, 1972; Roubik, 1979; Roubik 1983; Sakagami *et al.* 1983). Most stingless bees build their nests in empty trunks or in hollow branches. Some species use mainly dead trees. Even though the great majority of species use closed cavities to build their nests, some build completely exposed nests (aerial nests, only in the Neotropics). Some species of the genus *Trigona* establish their nests within the above-ground nests of termites and ants (Sakagami *et al.*, 1989). Camargo and Pedro (2002) list *Syntermes*, *Nasutitermes*, *Amitermes*, *Termes* and *Constrictotermes*, as Neotropical hosts, and also the large mound of nesting debris surrounding a colony of attine (leaf cutter) ants. Some stingless bees construct underground nests using naturally abandoned ant nests and cavities under plant roots. A few stingless bees build their nests inside active termite nests, such as termite mounds. Most of these stingless bees belong to primitive groups such as *Scaura latitarsis*, *Melipona quadrifasciata*, *Melipona bicolor* and *Tetragonisca angustula*, *Meliplebeia*, *Plebeia*, and *Nogueiraps* and some species of *Partamona*.

Some large genera display considerable species-level variation in nesting habit, likely produced by adaptive radiation. Large variation occurs, for example, within the Neotropical genus *Plebeia*. The nest sites and architecture include nesting habits on tree trunks, in crevices within rocks, in holes made by other animals, in hollow stems (including tree trunks) and in active termite nests (Michener, 1961).

Some other species build an exposed nest 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, and the species that have been introduced to new areas belong to this type. Some species of *Partamona* build semi-exposed nests in large cavities, bushes and abandoned bird nests.

Michener (1961) described the nests of of *Trigona* and the variety of structural features that result from the activity of thousands of worker bees.

Michener distinguished three types of nests:

(1) Living tree cavity: Most stingless bees build their nests in empty trunks or in hollow branches. Some species use mainly the dead trees that can be found readily in forests. *Trigona fimbriata*, *T. itima* and *T. canifrons* are typical examples.

(1) Underground: Some stingless bees construct underground nests using naturally abandoned ant nests and cavities under plant roots. A few species (such as *T. collina* and *T. apicalis*) build their nests inside termite nests. Occasionally species take advantage of natural cavities in the rock and soil behind cliff faces and their entrances can be discovered under small rock overhangs.

(2) Artificial cavity: A number of species, e.g. *T. laeviceps*, will nest in situations such as cavities in buildings or boxes.

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 either by fanning their wings at the nest entrance to draw cooler air into the nest or by gathering water into the nest to spread over the comb (Michener, 1974).

Generally, being tropical, stingless bees are active all year round although they are less active in cooler weather. 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, such as *Torigona spinipes* and *T. duckei* are known to have the ability to regulate the nest temperature and then only within certain limits. Michener (1974) presented data for adult *T. carbonaria* workers demonstrating that the tolerance to low temperature is not as poor as that of other *Apis* honeybees; in addition *T. carbonaria* workers tolerate much higher temperatures than *Apis* species. Nevertheless *T. carbonaria* can not easily control the temperature in the hive. The leading reason stingless bees have not spread from tropical and subtropical areas into the temperate zone of their lack of tolerance to low temperatures.

Pobsuk (2006) studied the biology of stingless bees in Thong Pha Phum District, Kanchanaburi Province. The results showed that most nests were located at west-facing sites which were warmer than other sites.

5. Behavior of stingless bee

5.1 Defense mechanisms

As noted above, the sting is vestigial and non-functional but the bees have various and efficient means of defense for colonies. Stingless bees being eusocial may have very large colonies and can be formidable by way of mustering numerous defenders.

However, defensive responses to individual small predators, such as other insects that catch bees nearby to nests are rarely studied.

In a study of Panamanian colonies including 40 species, half showed no defensive biting behavior toward the human observer (Roubik, 1983). Bees were timid when approached and retreated within the entrance. It might be thought that stingless bee keepers might tend to select gentler species but this is not the case, with half of those stingless bee species well-known in Brazil able to actively defend nests from large vertebrates (Nogueira-Neto, 1970).

The most common mechanism of defense against vertebrates among stingless bees is the habit of getting through the hair and fur of the invaders and irritating by crawling into or trying to enter the eyes, ears and nose. Some species (*T. cupia* and *T. fuscipennis*) adopt aggressive ways of defense, like biting the intruder's skin with the mandibles and applying sticky resin carried in the mandibles or on the hind legs. Fire bees (all species) and a few others (reportedly *Melipona rufiventris* in Bolivia), emit a caustic liquid containing formic acid from the mouth. In the case of *Oxtrigona* this causes severe irritation when the bee bites. Other species release unpleasant odors from a mandibular secretion (*T. capitata*, *M. marginata*) (Michener, 2000).

Not surprisingly, most nests that are exposed and potentially easily, attacked by predators have aggressively defensive workers, regardless of bee size or phylogeny. An exception is the genus *Dactylurina* in Africa (Eardley, 2004), species

of which have exposed nests but lack of aggressive defensive behavior (Darchen, 1972).

Very few species, for example *Tetragonisca angustula* and *Tetragona clavipes*, regularly maintain hovering defenders outside the nest. Hovering “guard” bees may defend against the robbing bee, *Lestrimelitta* (family Melittidae) (Wittmann *et al.*, 1990), or against raiding individuals from other meliponine colonies (Sakagami *et al.*, 1993).

Other forms, perhaps with less effective self protection, nest in or beside nests of ants or termites, from which they presumably gain protection. Other species build their nests next to the nests of aggressive bees or wasps, and thus use their neighbors as a defense.

Such aggregations of bees, wasps, ants or termites allow pooled defense against large predators. It is well known that alarm pheromones promote colony defense behavior in honey bees. However, in stingless bees direct assault appears to provoke the defensive response by the bees. Direct molestation, rather than the release of alarm pheromone dispersed in the air, evokes multicolony attack in *Partamona peckolti* (Roubik, 1983). Numerous species of this genus are defensive (Camargo and Pedro, 2003). Group defense occurs among small meliponines such as *Hypotrigona* (Kajobe and Roubik 2006) and *Tetragonisca weyrauchi*, but not Asian *Tetragonula* or *Heterotrigona* (Starr and Sakagami, 1987) or *Scaura tenuis* (Kerr *et al.*, 1967), which form aggregations.

However, the most common strategy of defense by stingless bees 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 (Dollin and Heard, 1998).

5.2 Communication

Stingless bees have mechanisms by which a worker that finds a food source or a suitable place to build the nest (when swarming is imminent) is able to transmit this information to the other bees. The form of communication varies from one species to another (Michener, 1974).

Many species of stingless bees are able to communicate the location of a food source. They use a chemical secreted from the mandibular glands and sunlight for orientation. Foraging workers stop at intervals of a certain distance and leave scented spots (marks) 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.

A more complicated mechanism has been observed in *Scaptotrigona postica*, *Oxytrigona tataira*, *Geotrigona* spp. and some others. In *Scaptotrigona 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. (Cruz-Landim, 1968). The marks are made with a secretion from the mandibular glands. In *Melipona*, sound is used to indicate the distance to the food source while the workers follow the bee that discovered the source.

Some stingless bees have no mechanisms to indicate the location of a food source and only produce a low sound when they enter the nest, bringing the nectar and passing it to the others. In this case, the sound stimulates the bees and the odor of the food can help the workers to find its source. This sort of mechanism is found, for example, in *Frieseomelitta silvestrii*. Other bees such as *Tetragonisca angustula* and *Plebeia droryana* have an even more complex mechanism. When the bees arrive with food they run in a zig-zag inside the nest and produce a sound that stimulates the other workers to go out of the nest and search for the source that has the same odor as that brought to the nest.

In *Melipona quadrifasciata* and *M. merillae*, returning foragers produce sound impulses varying proportionally to the distance of the food source. In *Trigona carbonaria*, a foraging bee that has located a good food source marks it with a chemical scent to help other workers find it (Esch, 1965).

In *Partamona cupira* and other species of *Partamona*, a worker finds a food source and, after stimulating the other workers, goes out of the nest and back to the source being followed by some other workers. This guiding bee liberates a substance produced by the mandibular glands which helps the other workers orient while following.

6. Distribution

Stingless bees can be found in most tropical or subtropical regions of the world, including Australia, Africa, South-east Asia, and parts of Mexico and Brazil (Batra *et al.*, 1973; Sakagami, 1982; Michener, 2000). The majority of native, eusocial bees of Central and South America are stingless bees.

The estimated several hundred species of stingless bees are arranged into 21 genera. The status of the group has varied but recently it has been placed as a subfamily Apinae tribe Meliponini. The most important genera are *Melipona* and *Trigona*. *Melipona* consists of about 50 species and is confined to the Neotropical region but *Trigona* is the largest with about 130 species and is the most widely distributed. 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 species in Australia, Papua New Guinea, and the Philippines, and as many as 40 species are native to Africa. 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.

There are several hundred described species of stingless bees in tropical areas worldwide (Sakagami, 1982). However, species are not distributed equally within the tropics. Local and regional diversity is high in the Neotropics, where up to 60 meliponine species can be found in a single forest locality (Roubik, 1989). Asian communities generally have less than 30 species (Roubik, 1990).

Stingless bees represent 5 to 25% of the total bee species (Apoidea) present in the dry to wet, and less seasonal forests of America (Roubik, 1993).

Schwarz (1939) who studied the structure of nests and the identification of stingless bees in the Indo-Malayan region found 25 species, i.e. *Hypotrigona scintillans*, *Trigona apicalis*, *T. binghami*, *T. melanoleuca*, *T. peninsularis*, *T. collina*, *T. atripes*, *T. melina*, *T. fimbriata*, *T. itama*, *T. canifrons*, *T. thoracica*, *T. fuscibasis*, *T. latigenalis*, *T. sarawakensis*, *T. fuscobalteata*, *T. geissleri*, *T. alicae*, *T. pagdeni*, *T. pagdeniformis*, *T. iridipennis*, *T. vadezi*, *T. ferrea*, *T. laeviceps*, *T. minor*, *T. terminata*, *T. ventralis*, *T. doipaensis*, *T. flavibasis*, *T. nitidiventris* and *T. hirashimai*.

Michener (2000) noted that stingless bees are found in the tropics of the world (although not east of the Solomon Islands in the Pacific). To the south they extend into temperate regions. To the north they extend little beyond the Tropic of Cancer.

Kerr and Maule (1964) considered South America is considered to be the center of origin and distribution of stingless bees because it had 183 species against 32 in Africa, 42 in Asia including Indonesia and 20 in Australia, New Guinea and the Solomon Islands.

Baumgartner and Roubik (1989) studied the diversity of stingless bees in Peru. They found 2 genera and 4 species: *Melipona interrupta grandis*, *Trigona duckei*, *T. (Paratrigona) prosopiformia* and *T. (Scaura) latitasis*.

Sakagami (1978) studied the distribution of stingless bees in South East Asia, including Thailand, Lao PDR, Vietnam, Malaysia and Singapore and found 11 species.

Sakagami and Khoo (1987) studied the distribution of stingless bees in the south of Thailand and Malaysia and found 1 genus and 6 species: *Trigona itama*, *T. canifrons*, *T. melina*, *T. reepeni*, *T. pagdiniformis* and *T. pagdeni*.

Sakagami *et al.* (1990) studied the structure of nests and the identification of stingless bees in Thailand and recorded no fewer than 23 species. Subsequently found the first giant stingless bees in Asia (*T. fimbriata*).

Saiboon (1996) studied the biology and ecology of the stingless bees in the lower part of southern Thailand and recorded was *Hypotrigona scintillans* from Thailand for the first time. In total Saiboon recorded 2 genera and 9 species: *Hypotrigona scintillans*, *H. pendleburyi*, *T. laeviceps*, *T. fuscobalteata*, *T. ventralis*, *T. terminata*, *T. artipes*, *T. apicalis*, *T. intima* and *T. thoracica*.

Rajitparinya (2003) studied the diversity of stingless bees species in varying ecological habitats at Suthep-Pui National Park in Chiang Mai Province, in the north of Thailand and found a total of 7 species: *Trigona laeviceps*, *T. apicalis*, *T. collina*, *T. terminata*, *T. fimbriata*, *T. melanoleuca* and *H. scintillans*.

Michener and Boongird (2004) studied the diversity of stingless bees from southern Thailand and described a new species, *Trigona sirindhornae*.

Wattanachaiyingchareon *et al.* (2004) studied species diversity and nesting sites of stingless bees in Sup-Lungka Wild Life Conservation Area, Lopburi Province. They found 22 colonies representing 7 species of stingless bees: *Trigona apicalis*, *T. collina*, *T. fimbriata*, *T. fuscobalteata*, *T. laeviceps*, *T. terminata* and *T. latigentalis*. There was no dominant species and the study site had low species diversity. The similarity index showed differences between the species assemblages of stingless bees

in the mixed deciduous forest, bamboo forest and dry evergreen forest. This study used nest entrance characters to classify stingless bees species.

Klaskasikorn *et al.* (2005) collected stingless bees from the western, eastern and northern regions of Thailand between 2002 and 2003. Ten species of *Trigona* were identified and two species, *Trigona bighami* and *T. minor* were new records for Thailand.

Inson and Malaipan (2006) studied the diversity of stingless bees in Thong Pha Phum and found 11 species: *Trigona apicalis* Smith, *T. melanoleuca*, *T. atripes*, *T. canifrons*, *T. thoracica*, *T. terminata*, *T. ventralis*, *T. flavibasis*, *T. iridipennis* variety 1, *T. iridipennis* variety 2, *T. iridipennis* variety 3, *T. iridipennis* variety 4, *Hypotrigona scintillans*, *H. pendleburyi* and *H. klossi*.

Currently 35 species of stingless bees are recorded from Thailand (Appendix B Table 1).

7. Diversity of Stingless bees

Changes in the nature of land-use in recent decades have not only resulted in the dramatic decrease in total forest cover, but also in an increasingly skewed size-distribution of forest remnants. Forest fragmentation is an important process contributing to the present-day concern over the loss of biodiversity and species extinction rates (Tschamtker and Kreuss, 1999; Steffan-Dewenter, 2002).

Some recent studies have shown that the diversity and abundance of several animal taxa in agricultural landscapes declines significantly with increasing distance from native habitats (Klein *et al.*, 2002; Steffan-Dewenter, 2002; Schulze *et al.*, 2004). Although these declines might be intuitively explicable and expected from theory (MacArthur and Wilson, 1967), the degree of decline differs widely among taxa. Empirical studies of communities of species in different habitats provide some insight into the challenging biological questions raised by these observations.

Trap nests have been used to monitor selected bee species through time in several sites to record changes in the frequency and constancy of species across different habitat types (Frankie *et al.*, 1993; Buschini, 2005). These insects can be expected to reflect ecological change through their species richness and related parameters and through their ecological functions or interactions. Flower monitoring also has been used successfully to study bee communities in selected locations in the Neotropics (Heithaus, 1979; Wilms *et al.*, 1996). More recently honey-water baiting was introduced as a method by Wille (1962) who noticed that flowers and visiting bees are difficult to access in closed forest. The method consists of spraying diluted honey (honey-water) on ground-level vegetation. Bees, mostly Apinae, and other flower-visiting insects arrive after minutes or hours and consume droplets from the leaves. Although easily applicable, only few studies have used the method for bee surveys (Inoue *et al.*, 1990; Salmah *et al.*, 1990; Roubik 1993). Salmah *et al.* (1990) used honey-water spraying along with flower monitoring to study apid bee diversity along altitudinal and disturbance gradients in fragmented landscapes of Sumatra. Their study sites included primary lowland forest, plantations near to forest, and urban habitats. Twenty two of 29 apid species present in the research area were attracted to honey baits in variable numbers. Combining data from flower monitoring with those of honey-water spraying, the study found that high species richness and abundance of apid bees was associated with the proximity of primary forest habitats (Salmah *et al.*, 1990). This study demonstrated a negative correlation between habitat alteration and stingless bee diversity, but it is difficult to pinpoint the precise ecological factors responsible for the effect.

Liow *et al.* (2001) studied bee diversity along a gradient of disturbance in tropical lowland forests of Southeast Asia. Bees were collected by three yellow funnel traps and three yellow floating platforms on which Petri dishes were arranged. Various baits (honey solutions, sugar solutions and banana pulp) were deployed in December (1998) to test the feasibility of trapping and/or attracting bee individuals. The traps were set 50 m apart with funnels alternating with the Petri dishes. Some bees were trapped after entering the funnel or by the surface tension of the liquid. Both methods rendered the bees wet, making taxonomic identification

difficult. The average trap rate (and S.E.) were 9.0 (2.4) and 8.3 (4.3) for individuals/trap/day for funnel traps and Petri dishes respectively. Honey baiting on vegetation was also tested. Honey-salt-water and sugar-salt-water solutions of varying concentrations were prepared and sprayed on vegetation 1.2 m from the ground. There were three baiting spots of about 1 m in diameter for different concentrations of honey or sugar solutions. The baiting spots were about 10 m apart at each site. It was found that a solution of honey diluted in the ratio of 1: 2 (honey : water, V: V) and solutions diluted in the ratio of 1: 4 (honey : water and sugar : water), with salt concentration constant at 2 cm³ in 500 ml of solution sprayed on vegetation, did not have significantly different recruitment rates for different morphospecies of bees. It was also found that the method of baiting on vegetation was more efficient at attracting bees than that of baited funnels type traps and Petri dishes. During each check, approximately 20.0 ± 2.8 trigonid bees were counted at individual vegetation baiting spots.

Eltz *et al.* (2003) used honey-water baiting and nest surveys to compare the species richness and abundance of stingless bees in logged and unlogged forests in Sabah, Malaysia, and to attempt to tease out the ecological factors (especially food resources and available nesting sites) that have the most influence on stingless bee richness and abundance in undisturbed and regenerating forests.

8. Nest density

Most stingless bee nests in South-east Asian forests are found in association with large, living trees situated either in pre-existing cavity in the trunk or underneath the tree bases (Salmah *et al.*, 1990; Roubik, 1992). To date, only a handful of studies have addressed ecological factors that are potentially limiting stingless bee populations (Hubbell and Johnson, 1977). As noted above, colonies tend to be perennial and comprise between a few hundred and several thousands of workers (Roubik, 1979; Sakagami, 1982; Sakagami *et al.*, 1983b; Salmah *et al.*, 1990). Hubbell and Johnson (1977) intensively studied nest sites and nest dispersion of five species of stingless bees in a tract of dry - forest in Costa Rica. Here bee species were

rather indiscriminant in their choice of nest trees, and suitable cavities seemed not to be in short supply. Meliponine nest dispersion has received less attention in the Paleotropics, but emerging data from Bornean rain forests suggest that patterns are quite different to those found in Central America: nests of the more frequently encountered species are often aggregated in nest trees (Roubik 1996; Nagamitsu and Inoue, 1997; Eltz *et al.*, 2003).

Jongjitivimol *et al.* (2005) studied nest dispersion of a stingless bee (*Trigona collina* Smith) in a mixed deciduous forest in Thailand. The results (standard Morisita index of dispersion within the area studied) showed that the nests of *T. collina* are strongly clumped. The pattern of nest dispersion in this species probably ensures an adequate number of mates in their mating range.

Samejima *et al.* (2004) studied the effects of human disturbance on a stingless bee community in a tropical rainforest in Sarawak, Malaysia. Human disturbance of tropical rain forests changes pollinator communities indirectly as a result of changes in resource availability. Samejima *et al.* (2004) surveyed forest structure and flowering activity, conducted a nest census and a bait-trap survey of stingless bees, both in primary forests and in forests disturbed by logging and shifting cultivation. The densities of late successional trees and large trees (diameter at breast height >50 cm) were higher in the primary forests than in the disturbed forests. Stingless bees nest only in large trees, nest density was positively correlated with the density of large trees. However, they found no relationship between the numbers of foragers and floristic parameters. Some species preferred nesting in living dipterocarps, while others preferred dead trees.

9. Foraging strategy

Stingless bees collect pollen, nectar and propolis like honey bees. Most of the stingless bee species are polylectic, foraging on a wide range of crops for pollen.

All stingless bees visit flowers and some species are known to use floral resources (nectar and pollen) from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms *et al.*, 1996). Studies of flower visitation and pollen foraging demonstrate that dietary overlap between different stingless bee species is often high (Heithaus 1979; Ramalho 1990; Wilms *et al.*, 1996). This indicates high potential for interspecific competition for food.

In most Neotropical species (Roubik, 1982) and all Asian species brood is raised on pollen as the major source of protein (Sommeijer *et al.*, 1985). Both pollen and nectar from (floral and extra-floral nectaries) are collected in quantities by foraging workers and deposited in special storage pots within the nest. Food storage allows colonies to survive for months without incoming food (Roubik, 1989).

Growth, survival and reproduction of eusocial bee colonies are all dependent on efficient resource influx. Pollen and nectar form the most important components of social bee resources, but also the collection of water, resin and mud are important for colony survival. For bees, nectar serves as a source of carbohydrates for energy, and pollen as a source of protein, mainly for feeding larvae. Eusocial bees are thus totally dependent on flowering plants for their food.

Inson (2006) studied the resin and gum collecting behavior of 20 colonies of 7 species over a period of a year. The diversity of *Trigona* spp. and their resin and gum collecting behavior mostly depended on environmental factors. Behavioral differences in collecting occurred on alternative plants, times and seasons. The bees preferred to collect resin and gum from plants in 16 plant families including Anacardiceae, Dipterocarpaceae, Euphobiaceae, Hypericaceae, Meliaceae and Moraceae. During the rainy season, foragers collected resin and gum all day; however, collecting behavior changed during the dry season, when collections were made only in the afternoon and until late in the day.

Jongjitvimol *et al.* (2004) studied pollen food sources of the stingless bees *Trigona apicalis*, *Trigona collina*, and *T. fimbriata* in Phitsanulok, Thailand. Pollen

loads were sampled from bee baskets of forager bees returning to their colonies. In total, 2,160 pollen loads from bee baskets of forager bees were identified into 29 plant species of 18 families. *T. collina* was by far the most polylectic species collecting 29 plant species, while *T. apicalis* foraged on 20 and *T. fimbriata* only 16. This suggests that the small *T. collina* is the most important pollinator among the three species.

Jongjitvimol *et al.* (2004) studied factors affecting foraging behaviors and food resource partitioning of three *Trigona* species (*Trigona apicalis*, *T. collina* and *T. fimbriata*) in the Phitsanulok area. The results showed that physical factors (temperature, relative humidity and light intensity) affect foraging behaviors. Comparative studies among *T. apicalis*, *T. collina* and *T. fimbriata* found that these species have different foraging times and food pollens. Morphological study to examine the relationship between body size and foraging appendages among the three species found all characteristics were significantly different. The results of the food resource partitioning study correlated with competition theory in that these three *Trigona* species appear to avoid competition for limited resources, resulting in the coexistence of these species in the same habitat.

Eltz *et al.* (2001) reported *T. collina* in Sabah collecting large quantities of spores of a saprophytic fungus, possibly associated with mould growth on the fallen flowers.

10. Pollination efficiency

Forests in tropical areas include many entomophilous plants. Undoubtedly stingless bees are of the great importance for the pollination of many of these wild plants in addition to the tropical crops.

Stingless bees and their cousins, the Apinae, are the only two groups of highly eusocial insects that have been used intensively by humans for agricultural and industrial purposes. The management and exploitation of stingless and Apinae bees (meliponiculture and apiculture respectively) is feasible and advantageous owing to a

number of the specific characteristics of eusocial insects (e.g. colony-based biology, efficient exploitation of food resources, etc). The Apinae consists of fewer than 10 species including the Western or European honeybee, *Apis mellifera*, and the Oriental honeybee, *A. cerana*, both of which are well-known as beekeeping species. The Meliponinae contains more than 400 species in tropical and subtropical areas, only some of which so far have been used like honeybees.

The important genera for stingless beekeeping or meliponiculture are *Melipona* and *Trigona*. Crane (1992) listed 14 species of *Melipona* and 21 species of *Trigona* that have been used in the traditional way. *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 the entire tropical continental area, and their use in traditional hive beekeeping has been reported in tropical America and occasionally in Asia. The principal species introduced to Japan were *Trigona carbonaria* (for Australia), *T. fuscobalteata* (Thailand), *Melipona beecheii* (Mexico), *M. quadrifasciata*, *Tetragona angustula*, *Plebeia droryana* and *Scaptotrigona bipunctata* (Paraguay).

Stingless bees are generally characterized by their stings being atrophied and of little harm to beekeepers in contrast to those of honeybees. They are also known as good pollinators of various crops. In Thailand there have been attempts to screen stingless bees that are promising pollinators and are being kept in their native areas, for introduction into Japan, with the practical aim of pollinating crops.

In Japan, more than 700,000 greenhouses are used to grow crops, where no wind, rain, or wild pollinators are available. Around 120,000 colonies of *Apis mellifera* are used for pollination annually, but farmers would rather not manage the colonies by themselves because of the danger that their handling poses. Professional beekeepers do the job instead. Stingless bees are promising pollinators for the following reasons: they are harmless to beekeepers and greenhouse workers, visit a wide range of crops (polylecty), are tolerant of high temperatures, are active throughout the year, can be transported easily, and hardly pose any environmental

risks by escaping into and invading natural habitats as they would not survive the Japanese winter. In contrast to honey bees, 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. Colonies of *T. fuscobalteata* have been kept in an environmentally controlled chamber (10 m², 26°C, 13L: 11D with fluorescent lamps) and forage without problems if provided properly with flowering plants. (Amano, 1997). *T. angustula*, *T. bipunctata*, and *T. carbonaria* can also be successfully kept in the same conditioned chamber.

Sakagami (1958) introduced the concept of domestication of stingless bees first into Japan. Maeta . (1992) imported 7 species of stingless bees (*Trigona minangkabau*, *T. moorei*, *T. itama* from South-east Asia; *Nannotrigona testaceicornis*, *Plebeia droryana*, *T. angustula*, *T. barocoloradensis* from Brazil) with a view to testing them as pollinators of strawberries. They published a note stating that *N. testaceicornis* was the most effective pollinating species and that economical fruit production could be maintained by the introduction of colonies into glasshouses.

Stingless bees have been shown to be valuable pollinators of crops such as macadamias and mangoes. They may also benefit strawberries, watermelons, citrus, avocados, lychees and many others. Research into the use of stingless bees for crop pollination in Australia is still in its very early stages, but these bees show great potential (Dollin and Heard, 1998).

Stingless bee colonies have also been imported into 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.

Although there are limited data on the influence of pollination by stingless bees on crop yield, many species are considered useful for the pollination of crops. Pollination tests comparing stingless bees with honeybees and/or bumblebees have been performed. Two species each of stingless bees (*Trigona carbonaria* and

Scaptotrigona bipunctata), honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) were placed in greenhouses of white clover, *Trifolium repens*. White clover must be pollinated to produce seed. The results were somewhat poor and contrary to what were expected. As the control, bagged flower heads produced almost no seed. The average weights of flower heads produced by *T. carbonaria*, *S. bipunctata*, *B. terrestris* and *A. mellifera* were 4.7 g, 7.1 g, 16.6 g and 14.2 g, respectively, while the weights of yield per 0.75 m² were 4.0 g, 7.9 g, 19.4 g and 17.0 g thus, while the two stingless bee species do pollinate white clover, they are much less effective than honey bees or bumble bees.

Another experiment investigated the pollination of tomato plants under greenhouse conditions. The flowers of tomatoes, *Lycopersicon esculentum* do not produce nectar, and the specific shape of their anthers favors the bumblebee, which performs buzzing-pollination. The effect of bumblebees, *B. terrestris*, and stingless bees, *T. carbonaria*, on producing fruit was compared. One compartment of the greenhouse contained a colony of *B. terrestris* and another colony of *T. carbonaria*. It is well known that when *B. terrestris* visits tomato flowers, it leaves a bite-mark on the flower. *T. carbonaria* was found to visit the flowers very often and leave a similar bite-mark. Based on calculations of the number of bite-marked flowers, *B. terrestris* visited 82% of the flowers and *T. carbonaria* more than 95% (Amano, 1997).

11. Host plants

The pollen grain is the structure used to transport the male gamete (i.e. male DNA) to the female part of a flower. Pollen must be sufficiently protective to ensure that the male gametes reach their destination safely. The outer wall of the pollen grain (the exine) is made up of a very tough, unusual substance known as sporopollenin. The inner layer of the pollen wall is made of cellulose and is similar in form to a typical plant cell wall. Pollen grains are microscopic-usually about 15 to 100 microns -and just a pinch of pollen powder contains many thousands of grains. Pollen is transported by wind, animals and insects to the receptive female floral part (the

stigma) (Buchmann and Nabhan, 1996). The vast majority of the 300,000 known species of plants are specialized for pollination by insects. Insect pollination of plants has evolved together with the insects themselves, so plant and insects are mutually dependent. For stingless bees, pollen is the main source of protein, lipids, vitamins, minerals and some carbohydrate (Wahurst and Goebel, 1995; O'Toole and Raw, 1999). Most bees feed their larvae with pollen, and adult bees nourish themselves on pollen and nectar mixtures. It has been hypothesised that this use of proteinaceous nourishment by adult bees has been fundamental to the multiple evolution of social behavior in Apoidea (Hunt, 1982). Pollen collection by bees provides important pollination services for many plants, including economically valuable crops, ornamentals and native plant species (Buchmann and Nabhan, 1996).

Pollen types are highly distinctive and unique sets of characteristics usually make it possible to identify the plant family or even species from which the pollen originates. Pollen grains of grasses tend to be very similar, reflecting more recent evolution and their pollen grains are commonly only identified as "grass" in studies. The main features which distinguish one type of pollen from another are size, shape and ornamentation of the outer wall. Pollen grains come in a great diversity of shapes although most are basically spherical or oval or disc-shaped. Features of the outer wall include pores and furrows, e.g. grass commonly has one pore and no furrows, birch has three pores and no furrows, oak has three furrows with a pore in the middle of each one. The grain can have a meshed, granular, grooved, spined or striated surface or can appear very smooth.

Stingless bees are generally polylectic and forage on an array of food plants that provide some pollen and nectar over much of the year rather than being highly specialized flower visitors. On the population level some species are known to use floral resources from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms *et al.*, 1996). Niche overlap between different stingless bee species was frequently found to be high in studies of flower visitation, although some selectivity has been reported, at least on the sub-tribal level (Heithaus, 1979; Ramalho, 1990; Wilms *et al.*, 1996). Studies by Nagamitsu *et al.* (1999) in

Sarawak, Malaysia, using a canopy access system suggest that resource partitioning between species may be mediated by preferences of different species for foraging in different forest strata.

The analysis of colony pollen stores or forager pollen loads has proven to be a useful tool in assessing bee diet as it is independent of flower accessibility and allows for equally high resolution in the forest canopy and understory (Engel and Dingemans-Bakels, 1980; Ramalho *et al.*, 1989; Nagamitsu *et al.*, 1999). Sommeijer *et al.* (1983) studied pollen loads of homing foragers of stingless bees in farmland in Trinidad and found that the variability of pollen spectra was greater between two species of *Melipona* than between colonies of the same species. Nagamitsu *et al.* (1999) found quite pronounced seasonal fluctuations of the between-species similarity of pollen diets of five species of stingless bees and speculated that the amount of resource partitioning may be related to general pollen resource availability.

Kajobe (2007) studied pollen foraging by the stingless bees *Meliponula bocandei* and *Meliponula nebulata* and compared these species with *Apis mellifera*. Palynological results showed a considerable overlap among the three species. *A. mellifera*, which was the largest of the three bees (11 mm), had the highest diversity while *M. nebulata* had the lowest. Among the stingless bees, the larger *M. bocandei* (9 mm) had a wider pollen spectrum than *M. nebulata* (7 mm). The relatively bigger colony and body size of *A. mellifera* were positively correlated with pollen diversity. The recruitment technique to food sources was implicated as one of the factors accounting for the differences in pollen foraging behavior. Foragers of *M. nebulata* flew out in characteristically distinct bouts, directly leading nest mates to food sources (piloting). Pollen diversity of *A. mellifera* was lower during the rainy season than in the dry season while for *M. bocandei* and *M. nebulata* there was no seasonal variation. Pollen diets changed over the seasons probably because of the alternating nature of flowering plants. This led to the conclusion that different pollen foraging strategies could ultimately result in partitioning of food resources.

Study site

Thong Pha Phum Districts located in Kanchanaburi Province was selected as the survey area (Figure 3).

Thong Pha Phum District lies in the northern part of Kanchanaburi Province, central Thailand. The important water resource is the Khwae Noi River. The southern part is close to Khao Laem National Park, Kanchanaburi Province, and the western part is close to the Thailand-Myanmar border. It is a complex mountain area with a 150 km boundary with Myanmar. Thong Pha Phum consists of hill evergreen forest, dry evergreen forest and mixed deciduous forest.

Topography character

The major part of the area is complex mountain range, with the range running predominantly in a north-south line, under, be one (part) of Sau Pak Bung Mountain, there are a few low-lying plains. The area is between 100 metres and 1,249 metres above sea level. At 1,249 metres, Chang Phak Mountain in the west is the highest point. Other important peaks are, for example, Nisoa Mountain, Puthong Mountain, Pak Mountain, and Chalong Mountain. These peaks are the origin of all gullies and streams, such as Malay Brook, Kob Brook, Pak Kok Brook, Jet and Metr Brook, all of which flow down to the east plain, to Koa Lam Dam, and eventually to the Khaiw Noi River

Climate

The area has a kind of tropical climate which receives influences from the south-eastern monsoon in the rainy season and the north-eastern monsoon in winter. The seasons include summer from February to April, the rainy season from May to October, and winter from November to January. The maximum temperature is 33 °C; the minimum temperature is 8° C. The average rainfall is 1,760 mm/year with the maximum of 2,016 mm in September. Relative humidity averages 85.67%.



Figure 3 Map of Kanchanaburi Province, Thailand.

Source: Modified from Anonymous (2008)

Flora and Fauna

Flora

Thong Pha Phum District basically comprises four forest types:

1) **Evergreen forest:** The dominant trees are *Homonoia odorata* Roxb. (F. Euphorbiaceae), *Dipterocarpus grandiflorus* (Blanco) (F. Dipterocarpaceae) etc. with an understorey of rattan, ferns and screw pine.

2) **Dry evergreen forest:** The dominant trees are *Dipterocarpus turbinatus* C.F. Gaerth (F. Dipterocarpaceae), *Toona ciliata* M. Roem (F. Meliaceae), *Mangifera caloneura* Kurz (F. Anacardiaceae) etc. Understorey of palm, galingale, and ferns, etc.

3) **Upper mixed deciduous forest:** Dominant trees include *Carpinus viminea* Wall (F. Betulaceae), *Magnolietia garrettii* Craib (F. Magnoliaceae). Understorey of mosses, ferns, etc.

4) **Dipterocarp forest.** Dominant trees include *Pterocarpus macrocarpus* Kurz (F. Papilionoideae), *Syzygium glaucum* (F. Myrtaceae), *Azalia xylocarpa* (Kurz) (F. Caesalpinoideae), *Lagestroemia speciosa* (L.) Pers. (F. Lythraceae), *Diospyros mollis* Griff (F. Ebenaceae). Understorey of bamboo, etc.

Fauna

Thong Pha Phum District is an important and rich habitat for wild animals, Because the forest is continuous with other forests and reserves, namely Thung Yai Naresuan Wildlife Sanctuary, Sai Yok National Park, Khao Laem National Park and Myanmar it supports wildlife that prefer to move and wildlife that migrates regularly. There are no civilians in the forest and many areas are little disturbed so that it is possible to see regularly, for example, forest elephant, mountain goat, deer, barking

deer, chevrotain, wild boar, bear, monkey, gibbon, palm civet, fishing cat, tiger, Malayan bear, rat, mongoose, bat, hare, wild cat, porcupine, hornbills, swallow, hawk, heron, eagle, owl, ground lizard, centipede, scorpion, millipede, snail, leech, snapping turtle, frog, small toad, toad, bullfrog, eel, bison fish, freshwater fish and etc. The invertebrate fauna remains largely undocumented.

MATERIALS AND METHODS

Materials

1) Materials for collecting and preserving specimens:

- Insect net
- Killing jar
- Cardboard, paper or plastic box
- Ice box
- Vials
- Insect pins (number 3)

2) Material for survey behavior of stingless bees

- Digital Camera
- Watch
- Binocular

3) Material for study of diversity of host plants

- Slides and cover slips
- Centrifuge
- Lactophenol
- Microscope (compound, dissecting, magnification required)
- Thermometer
- GPS (Global Positioning System) Unit
- Light Microscope

4) Chemical

- 10% potassium hydroxide (KOH)
- Glacial acetic acid
- Sulfuric acid (H₂SO₄)
- Acetic acid
- 95% ethanal
- Absolute ethanol
- Benzene
- Silicone oil

Methods

Study sites and nest searching

Stingless bees were studied at the four forest sites (Figures 4 - 8) given below. The lists of plant species in each forest type are based on surveys by Wongprom (2005) and Insoon (2006)

Dry dipterocarp forest (DDF) (449 m above sea level and 14.41°N, 098.29 °E) (Figure 5). *Shorea roxburghii* G. Don, *Shorea obtusa* Wall. ex Blume, *Shorea siamensis* Miq., *Aporosa villosa*, *Memecylon* sp., *Dipterocarpus* spp. , *Dipterocarpus obtusifolius* Teijsm. ex Miq., *Dipterocarpus tuberculatue* Roxb., *Suregada multiflorum* (A. Juss.) Baill., *Aporosa villosa* (Wall. Ex Lindl.) Baill, *Lithocarpus thomsonii* (Miq.) Rehder, *Lithocarpus lindleyanus* (Wall), *Castanopsis indica* (Roxb.) A. DC., *Castanopsis tribuloides* (Sm.) A. DC., *Quercus kerrii* Graib, *Cratoxylum formosum* (Jack) Dyer, *Careya arborea* Roxb., *Xylia xylocarpa* var. *keri* Craib&Hutch.

Upper mixed deciduous forest (UMDF) (549 m above sea level and 14.42°N, 098.28 °E) (Figure 6). *Dipterocarpus tubinatus* Gaertn. f., *Shorea roxburghii* G. Don, *Pterocarpus macrocarpus* Kurz, *Lithocarpus annamensis* A.

Camus, *Garuga pinnata* Roxb., *Pterospermum semisagittatum* Buch-Ham., *Dillenia obovata* (Blume), *Antidesma ghaesembilla* Gaerth., *Gigantochloa albociliata* Munro, *Gigantochloa hasskarliana* Back.ex k. Heyne, *Bambus tulda* Roxb., *Psydrax nitida* (Craib) K.M. Wong, *Chromolaena odoratum* (L.) R.M. King & H. Rob., *Oroxylum indicum* (L.) Kurz, *Garuga pinnata* Roxb., *Peltophorum dasyrachis* (Miq.) Kurz, *Siphonodon celastrineus* Griff., *Siphonodon celastrineus* Griff., *Terminalia triptera* Stapf, *Terminalia bellirica* (Gaerth.) Roxb., *Terminalia alata* Roth, *Anogeissus acuminata* (Roxb. Ex DC.), *Anisoptera costata* Korth., *Aporosa villosa* (Wall. Ex Lindl.) Baill, *Croton roxburghii* N.P. Balakr., *Aporosa octandra* var. *yunnanensis* (Pax&K. Hoffm), *Glochidion sphaerogynum* Kurz, *Bischofia javanica* Blume, *Mallotus philippensis* Mull. Arg., *Dalbergia oliveri* Gramble, *Casearia grewiifolia* Vent., *Exacum tetragonum* Roxb., *Milletia brandisiana* Kurz, *Schima wallichii* (DC.) Korth., *Lithocarpus polystachyus* (A. DC.) Rehder, *Siphonodon celastrineus* Griff., *Barringtonia acutangula* (L.) Gaertn., *Peltophorum dasyrachis* (Miq.) Kurz, *Albizia odoratissima* (L.f.) Benth., *Lannea coromandelica* (Houtt.) Merr., *Psydrax nitida* (Craib) K.M. and *Hymenodictyon orixense*

Lower mixed deciduous forest (LMDF) (167 m above sea level and 14.39°N, 098.31 °E) (Figure 7). *Miliusa velutina* (Dunal) Hook.f.&Thomson, *Cananga latifolia* (Hook.f.&Thomson), *Wrightia arborea* (Dennst.) Mabb., *Amorphophallus* sp., *Vernonia volkameriifolia* (Hosseus), *Oroxylum indicum* (L.) Kurz, *Fernandoa adenophylla* (Wall.ex G. Don) Steenis, *Markhamia stipulate* Seem. Var. *Stipulata*, *Stereospermum neuranthum* Kurz, *Bombax ceiba* L., *Garuga pinnata* Roxb, *Protium serratum* Engl., *Cassia fistula* L., *Cassia siamea* (Lam.) Irwin&Barneby, *Saraca indica* L., *Siphonodon celastrineus* Griff., *Anogeissus acuminata* (Roxb. ex DC.) Guill.&Perr., *Terminalia alata* Heyne ex Roth, *Diospyros ehretioides* Wall. ex G. Don, *Elaeocarpus sphaericus* (Gaertn.) K. Schum., *Croton roxburghii* N.P. Balakr., *Lagerstroemia villosa* Wall, *Terminalia bellerica* (Gaertn.) Roxb., *Xylia xylocarpa* var. *kerrii* (Craib & Hutch), *Careya sphaerica* Roxb., *Aporosa villosa* Wall., *Croton poilanei* Gagnep, *Oroxylum indicum* (L.)Kurz, *Antidesma bunius* (L.)Spreng., *Bambusa burmanica* Gamble., *Bischofia javanica* Blume, *Antidesma ghaesembilla* Gaertn., *Trewia nudiflora* L., *Phyllanthus emblica* L.,

Cleidion spiciflourum (Burm.f.)Merr, *Antidesma sootepense* Craib, *Antidesma acidum* Retz., *Casearia grewiiifolia* Vent., *Dendrocalamus strictus* (Roxb.)Nees, *Cratoxylum cochinchinense* (Lour.) Blume, *Engelhardtia spicata* Blume var.spicata, *Litsea monopetala* (Roxb.) Pers., *Careya arborea* Roxb., *Millettia leucantha* Kurz, *Lagerstroemia tomentosa* C. Presl, *Lagerstroemia calyculata* Kurz and *Ficus benjamina* L.

Dry evergreen forest forest (DEF) (362 m above sea level, and 14.33°N, 098.33 °E) (Figure 8). *Parashorea stellata* Kurz, *Xerospermum intermedium* Radlk. *Dipterocarpus baudii* Korth, *Diospyros* sp., *Xerospermum noronhianum* (Blume), *Millettia* sp.1, *Aglaia ubiginosa* (Hiern), *Pterocymbium tinctorium* (Blanco), *Knema linifofia* Roxb., *Millettia atropurpurea* Wall., *Aglaia* sp., *Dipterocarpus baudii* Korth., *Arpocarpus* spp., *Payena* spp., *Cryptocaya* sp., *Palaquim* sp., *Bhesa robusta* (Roxb.), *Chisocheton siamensis* Craib, *Beilchimiedia* sp., *Shosea* sp., *Mangifera cochinchinensis* Engl., *Ceriscoides turgida* (Roxb.), *Diospyros dasyphylla* Kurz, *Ficus vasculosa* Wall. ex Miq., *Bridelia retusa* (L.), *Alocasia macrorrhizos* (L.) G. Don) and *Elaeocapus* sp.

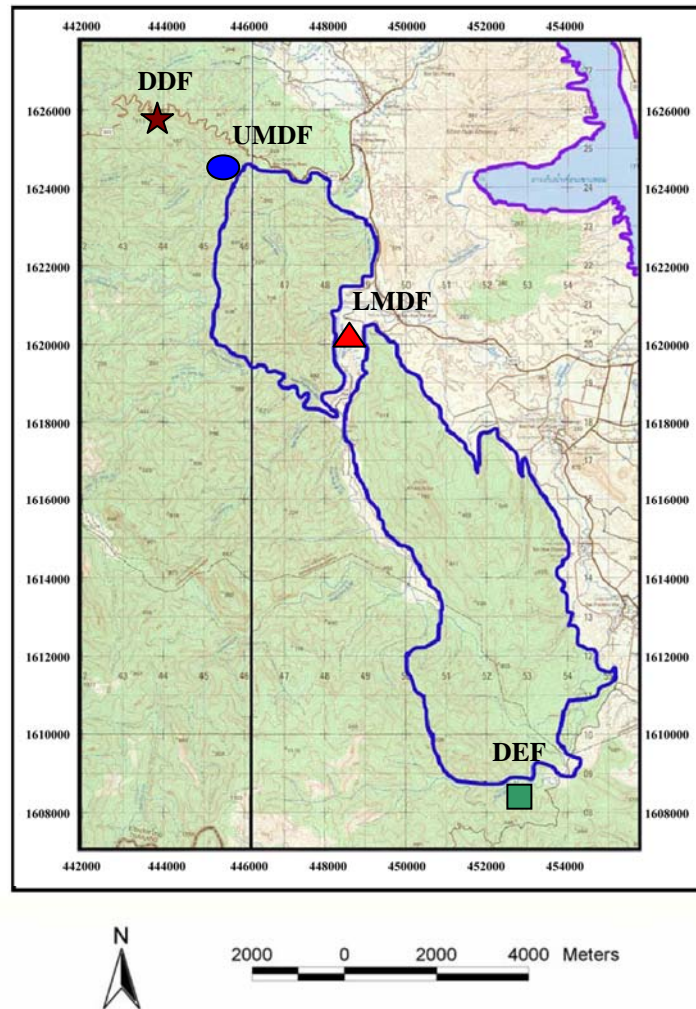


Figure 4 Study sites; dry dipterocarp forest (DDF), upper mixed deciduous forest (UMDF); lower mixed deciduous forest (LMDF) and dry evergreen forest (DEF), were located in Thong Pha Phum District, Kanchanaburi Province.

Source: modified from Inson (2006)



Figure 5 Photograph of dry dipterocarp forest (DDF).



Figure 6 Photograph of upper mixed deciduous forest (UMDF).



Figure 7 Photograph of lower mixed deciduous forest (LMDF).



Figure 8 Photograph of dry evergreen forest (DEF).

1. Comparisons between stingless bee capturing methods

Preliminary studies were conducted from January to March 2004 to optimize sampling methods. The experiment was designed in a randomized complete block design (RCB) with eight replicates (treatments) and thirty plots in four types of forest, including DDF, UMDF, LMDF and DEF.

Treatments (sampling methods)

- 1) Salt solutions (SaS)
- 2) Sugar solutions (SuS)
- 3) Honey solutions (HS)
- 4) Honey solution with salt (HSaS)
- 5) Fish sauce (FSa)
- 6) Yellow pan trap: plastic pan containing only detergent and water (YPT)
- 7) White pan trap: plastic pan containing only detergent and water (WPT)
- 8) Blue pan trap: plastic pan containing only detergent and water (BPT)

All methods were set up as follows:

All bait solutions (honey solutions: honey and water in the ratio 50: 50 by volume; sugar solutions: sugar sucrose 200 gram and water 500 ml; honey solution with salt: honey and water in the ratio 50: 50 by volume with salt 2 mg; fish sauce Trade name: Tippiaros 500 ml) were prepared and sprayed on vegetation 1-2 m from the ground at each site. The baiting spots were about 10 metres apart at each of the sites.

Pan traps of three different colors (yellow, white, and blue) were set up to test the feasibility of trapping or attracting bee individuals at each site. Pan traps were placed on the ground at each site.

All treatments were started from 8.00 a.m. and 9.00 a.m. and a circuit of survey stations was completed after approximately 90 minutes. Bees were recorded at the spray stations during a second circulation that started 150 minutes after spraying was initiated, and was completed within 240 minutes. Bees attracted to each of these baited spots were caught with a standard insect net, during a maximum period of five minutes. I waited at each baited spot for 2 minutes to scan the area for bees and moved on if there were none. The collected bees were identified following the key for Sumatran species given by Sakagami *et al.* (1985) and Indo–Malayan species given by Schwarz (1939).

Data analysis

Statistical analysis was carried out using the statistical software IRRI. The differences in abundance (number of individual) of bees between methods were tested by analysis of variance (ANOVA). Duncan's new multiple range tests was used to determine if the catch-rate of stingless bee species and the number of stingless bee individuals in the four types of forest were significantly different.

2. Surveys of diversity of stingless bees

- Sampling procedure and data collection

Four representative sites were selected. At each site we established a transect grid covering an area of 100 x 100 m.

Bee surveys

Honey bait traps: Honey baiting on vegetation. Honey-alt-water (solution of honey diluted in the ratio of 1:1 honey: water; volume: volume, with salt concentration constant at 2 cm³ in 500 ml of solution) were made and sprayed on vegetation 1-2 m from the ground at each sites. The baiting spots were about 15 m apart at each site.

For the actual bee surveys, one to three transects of 0.5-1 km were set-up at each site. Honey solution (1:1, honey: water) with 2 cm³ salt/500 ml of solution, standardized with a hand refractometer was used to attract bees. Thirty jets (each of 100 ml) of this solution were sprayed on the vegetation marked with colored flagging tape every 15 m along the transects. The baiting spots were about 1 m in diameter and between 30-100 cm above the ground (Figure 9).

Bees (principally Apidae) attracted to each of these baiting spots were caught with a standard insect net, during a maximum of five minutes. I waited at each baiting spot for 20 seconds to scan the area for bees and moved on if there were none. The collected bees were identified following the key for Sumatran species given by Sakagami *et al.* (1985) and Indo – Malayan species given by Schwarz (1939).

Spraying started between 8.00 am. and 9.00 am. and was completed after approximately 90 minutes. Bees were recorded at the spray stations during a second circulation that started 150 minutes after spraying was initiated, and was completed within 240 minutes. This time schedule had proven to yield maximum numbers of species and individuals of stingless bees during previous tests. Normally bees could be identified directly at the stations. In uncertain cases vouchers were collected and later identified using published keys and descriptions (Schwarz, 1937, 1939; Sakagami, 1978; Sakagami and *et al.*, 1985, Rinderer *et al.*, 1989; Sakagami *et al.*, 1990). Honey-spraying was scheduled to take place mostly on clear or slightly cloudy days. If there was afternoon rainfall before completion of the assay, the accumulated data were discarded and the assay was repeated on a different day.

Air temperature and humidity data were recorded for each forest type of each month using a thermohydrograph and dry-and-wet bulb psychrometer. Light levels were obtained by fish-eye photography (Inson and Malaipan, 2006).

Data analysis

2.1 Species richness and abundance of stingless bee species

Measures of bee diversity and abundance can be analyzed as follow: the number of bee species per forest, and the number of bee individuals. All three measures were analyzed for stingless bees. ANOVA with repeated measures design was used to test for effects of forest type and year on abundance.

2.2 Seasonal change of the dominant species

Data analysis by Sorensen similarity index:

Similarity of species composition between the monthly samples using Sorensen similarity index.

Sorensen similarity index = $2W/(A+B)$

W = The species richness shared between sample A and B

A = The species richness of sample A

B = The species richness of sample B

2.3 Diversity indices and evenness of stinglee bee species

Species diversity of stingless bees were analyzed by using the Shannon-Weiner diversity index (Shannon and Weiner, 1949; Price, 1984).

$$H' = - \sum_{i=1}^s p_i \log p_i$$

where s = the number of species, p_i = the proportion of the total number of individuals consisting of the i th species and H' = an estimate of the diversity of the total population of individuals. Diversity indices were calculated based upon the number of stingless bees of each species found in each type of forest.

To find evenness, H_{max} must be calculated. That is the diversity index would be if all species in the community had an equal number of individuals. This number can be calculated by;

$$H_{max} = \ln S$$

Where; \ln = natural log

S = number of species

Thus, Evenness (J) is determined by

$$J = H. / H_{max} \text{ (Pielou, 1975)}$$

Similarity by Jaccard

Stingless bee data from the four types of forest were subjected to a cluster analysis using PC-ORD version 2.0. This analysis used Jaccard distance and Ward's method. Jaccard's Index is calculated as follows: The number of species found in both pair of samples is expressed as a percentage of the total number of species found in one or the other of the samples. In Ward's method, algorithms join clusters in such a way that within-group variances are minimized. This method uses Euclidean distances, which, in this case, is between forest types. In this study, the data consisted of abundance data for all species across all four forest types (McCune and Mefford, 1995).

Cluster analysis

To determine the factors affecting the distribution of stingless bee species, canonical correspondence analysis (CCA; Braak, 1986) in PC-ORD version 2.0 (McCune and Mefford, 1995) was performed using data matrices of log-transformed stingless bee species abundance (numbers of individuals) data and the two environmental variables recorded. Axis scores were standardized using Hill's (1979) method and scaled to optimize the representation of species. CCA is a particularly appropriate method for analysing a site/species matrix where environmental variables have been measured for each site.



Figure 9 Photograph of honey – bait traps.

3. Study of nest density of stingless bees

Study sites and nest searching

During 12 months in the working site during April 2004 to March 2005, I searched for stingless bee nests in all four research localities. Nests were located by inspecting trees along forest trails and by standardized nest surveys along transect grids established for quantitative measurements of stingless bee nest density. Data sets were pooled for the analyses presented below.

3.1 Nest aggregation and nest density and nest trees

Nest surveys

Nests of stingless bees of South-east Asian forests are found in cavities in tree trunks or underneath the bases of trees. In order to quantify nest density in my sites I searched for bee traffic and nest entrance tubes in the bases and trunks of all trees larger than 30 cm dbh. situated in 20 m-corridors along the established transects. Nest counts were transformed into nest density per hectare by incorporating area searched (length of transect x 20 m). The total area searched was 1 ha. per site. Nest trees and individual nests were marked with spray paint and flagging tape. Whenever possible bee species identifications were made at the site; otherwise voucher specimens were collected. In the case of colonies high up in trees, identifications could normally be made by inspection of bee size and color as well as by observing with binoculars the characteristic shape of the resinous entrance tubes.

For bee nests and nest trees the following data were recorded:

- 1) Bee species: Identification of hand-netted vouchers was performed using descriptions of Indo – Malayan species given by Schwarz (1937), and the key for Sumatran species given by (Sakagami *et al.* 1985).

2) Nest type: We distinguished two general modes of nesting “cavity nests” were situated within hollows in the tree trunks and are characterized by entrance tubes emerging from those hollows via openings in the wood. Cavity nests could be at any height of the tree trunk. “base nests”, on the other hand, were always situated under or at the bases of trees and are characterized by an entrance tube attached to the outer wall of the tree base, running down the tree until concealed from sight by surrounding soil. Most base nests are probably located within the upper root system of the tree, but in some cases the entrance tube may also curve up into the lower section of the trunk, which is frequently hollow in large trees (Panzer, 1976).

3) Diameter of nest trees: Diameter at breast height was measured (using measuring tape) or estimated by comparison with machetes of known length. In the case of trees with large buttresses dbh-recordings were made for the height above the buttresses.

4) Taxonomy of nest trees: Trees were either identified in the field by experienced forestry staff, or, in most cases, using fallen leaves originating from the respective trees. Leaf samples were identified by botanists (Department of Forestry).

4. Diversity of host plants

4.1 Studies of foraging behavior

I studied foraging behavior of seven species of stingless bee in the four types of forest in the wet and dry seasons as follows:

1) Dry dipterocarp forest (DDF)

One nest of *Trigona apicalis*.

2) Upper mixed deciduous forest (UMDF)

Four nests representing *T. apicalis*, *T. collina*, *T. ventralis* and *T. terminata*.

- 3) Lower mixed deciduous forest (LMDF)
Five nests representing *T. apicalis*, *T. melanoleuca*, *T. canifrons*,
T. collina and *T. sirindhornae*.
 - 4) Dry evergreen forest (DEF)
Two nests of *T. apicalis*.
- The seven stingless bee species studied of foraging behavior have been divided by size into three groups:
 - Large size : *T. apicalis*, *T. melanoleuca* and *T. canifrons*
 - Medium size : *T. collina* and *T. terminata*
 - Small size : *T. ventralis* and *T. sirindhornae*

The number of stingless bees going out of the nest entrance within a 15 minutes interval was recorded for each nest in the four types of forest. All counts were made between 9.00 a.m. and 5.00 p.m. Counts were taken twice in each season.

4.2 Pollen foraging behavior

Returning pollen foragers of stingless bees were captured at the nest entrances using an insect net. This was done by briefly closing the entrance to the nest and randomly capturing 20 foragers that had pollen loads and gum. After removal of their pollen loads with a blunt needle the workers were released. The pollen clusters from each day's collection were stored together in a sealed, glass vials. For any given date, pooled 20-forager samples were collected from each colony between 9.00 a.m. and 5.00 p.m. Sampling was done from the same nests which were studied for foraging behavior and took place in all four types of forest (DDF, UMDF, LMDF and DEF). Repeated samples were taken every weeks from April 2004 to March 2005. Thus, pollen was collected every weeks for one year. For all samples, the number of stingless bees that had collected pollen was recorded. These data were used to calculate the percentage of returning foraging stingless bees that had collected pollen.

4.2.1 To compare the pollen foraging of one species of stingless bee (*Trigona apicalis*) across four types of forest.

4.2.2 To compare the pollen foraging of all species of stingless bees from four types of forest.

5. Palynology: pollen treatment and analysis

Standard palynological protocols (KOH digestion, acetolysis, glycerin jelly mounting) were followed for slide making (permanent slides were prepared by the Erdtman method).

Acetolysis procedure

- 1) A hot plate was set up and a water bath brought to boiling.
- 2) Floral anthers were placed in 15 ml polyethylene test tubes.
- 3) To each test tube 5 to 10 ml of 10% KOH was added and the mixture was stirred with a glass rod. The test tube was then placed in the boiling water bath for 2-3 minutes.
- 4) The test tube was removed from the water bath and the contents sieved through a 200 mm stainless steel screen into a beaker.
- 5) The anthers were pressed gently into the screen with a spatula and the screen was rinsed thoroughly into a beaker. The beaker contents were transferred to centrifuge tube, and then centrifuged. The tube was decanted and the supernatant discarded.
- 6) The sample was washed with distilled water, centrifuged and again decanted. This was repeated 2-3 times.

7) After the final distilled water supernatant had been discarded 10 ml of glacial acetic acid were added to the sample, which was again centrifuged and decanted.

8) After the initial glacial acetic acid wash had been discarded 5 to 10 ml of acetoysis mixture was added the sample (acetoysis mixture is made by mixing 9 parts glacial acetic acid with 1 part concentrated sulfuric acid). The sample plus acetoysis mixture was stirred and placed in the boiling water bath for 1-2 minutes.

9) The sample was removed from the bath, centrifuged and decanted.

10) The sample was washed with distilled water 2-3 times.

11) Another 10 ml of distilled water was added and the mixture stirred with a glass rod, centrifuged and decanted.

12) The sample was dehydrated with 95% ethanol, centrifuged and decanted. The sample was then washed with absolute ethanol, centrifuged and decanted.

13) Finally the sample was washed with benzene, centrifuged and decanted.

14) The pollen sample was transferred to a tube to which were added 1-2 droplets of silicone oil.

- In each of the above steps centrifuging was performed for 1 minute at 3,000 RPM.

Preparation of slides for Light Microscopy (LM)

Glycerin jelly mounts were prepared by adding a drop of concentrated pollen to a piece of glycerin jelly on a slide. The slide was warmed slowly and the jelly mass stirred to mix. A cover glass was lowered carefully over the droplet and sealed with nail polish around the edges. Slides were stored flat to avoid loss of pollen.

The slides were analyzed and pollen characteristics recorded in a standardized way pollen size.

Digital images were made from polar and equatorial views of all pollen types and images were entered into a pollen database that served as a working reference. Taxonomic identifications of types were made to the level of plant family, genus or species.

6. Flowering phenology

In an attempt to quantify the floral resource availability in the habitat, I repeatedly ran a 1 km flower phenology transect that criss-crossed through the nesting area of the bees. I counted all visible flowering, woody plants from the transect and collected specimens to assess species. In the case of large trees binoculars were used to confirm the presence of flowers and decayed flowers were collected from the forest floor. Assessment of flowering activity normally took place immediately following pollen sampling. Due to its limited scope and the lack of canopy access the transect was likely to miss much of the actual flowering in the area. Therefore, the results should be regarded as an index of flowering intensity and diversity rather than a complete survey of potential bee resources.

The number of mass-flowering plants in bloom for each plant species was recorded every week. The numbers of mass-flowering plants in bloom within the circumference of 500 m were added together to give “the number of mass - flowering plants in bloom” which was used as a weekly measurement.

During the sampling periods (April 2004 to March 2005), the dry season was April 2004 and October 2004 - March 2005, while the wet season was from May 2004 until September 2004 (Figure 10).

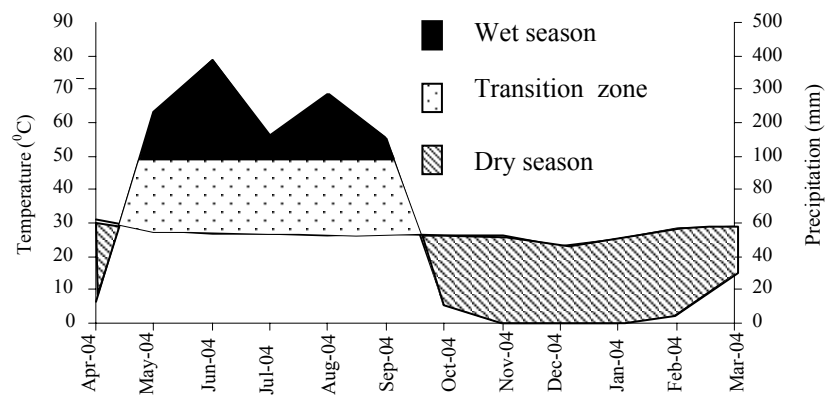


Figure 10 Seasonal changes in air temperature and precipitation in four types of forest during April 2004-March 2005 at Thong Pha Phum District, Kanchanaburi Province.

Source: The Meteorological Department.

RESULTS

1. Comparisons between stingless bee capturing methods

The mean numbers of stingless bees were caught by all methods all sites (DDF, UMDF, LMDF and DEF) were 6.9, 5.0, 4.6 and 1.3 individuals respectively. The honey solution mixed with salt bait trap method was significantly more efficient at catching bees than any other method (T4: HSaS, Table 1).

Table 1 Treatment (Average over 30 replications) Mean catches (all bee species combined) by each method (30 replicates).

Treatment	DDF	UMDF	LMDF	DEF
T1 (SaS)	2.5 d	2.1 d	1.6 d	0.6 c
T2 (SuS)	5.2 c	4.6 c	4.3 c	1.9 b
T3 (HS)	12.2 b	9.8 b	9.6 b	1.9 b
T4 (HSaS)	22.0 a	13.1 a	12.0 a	2.9 a
T5 (FSa)	5.9 c	4.6 c	3.6 c	1.2 c
T6 (YPT)	3.0 c	2.3 d	1.7 d	0.8 c
T7 (WPT)	2.1 d	1.8 d	1.7 d	0.7 c
T8 (BPT)	2.2 d	2.0 d	1.9 d	0.8 c
T9 (Control)	0	0	0	0
Mean	6.9	5.0	4.6	1.3

In each column, means identified by similar letters (a, b, etc) are not significantly different.

The mean numbers of stingless bees were 6.9 individuals (DDF), 5.0 (UMDF), 4.6 (LMDF) and 1.3 (DEF). In all forest types the honey solution mixed with salt bait trap method was significantly more efficient at catching bees than sugar solutions, honey solutions, salt solution, fish sauce, or yellow, white and blue plastic bowls (Duncan's multiple range tests; see Appendix B Table 2-5).

Overall, the performance of the each collecting method was more or less consistent across the four forest types. (see rankings in Table 1). As noted above, honey solution with salt (T4) was consistently the best attractant. Honey solution alone (T3) was consistently the second-most efficient collecting method, and the sugar solution (T2) and the fish sauce (T5) tended to alternate as the third-most efficient collecting method. Salt alone (T1), and the white (T7) and blue (T8) pan traps tended to be the least efficient collection methods.

2. Taxonomic studies of stingless bees in Thong Pha Phum District, Kanchanaburi Province, Thailand

Stingless bee samples from the study area were identified into morphological species by using the identification keys of Schwarz (1939) and Sakagami (1985). Fifteen species, 7 subgenera (and informal groups-see below) and 3 genera were represented among the samples (Table 2).

There is still no unanimous agreement on the subgeneric classification of the genus *Trigona*. The present study follows Sakagami's (1961) long-term studies of the Asian stingless bees, which have strongly influenced most recent authors, e.g. Eltz (2001). Accordingly, I have retained several species in the subgenus *Tetragonula*, even though Michener (1990) has placed this subgenus within the subgenus *Heterotrigona* Schwarz. Dollin *et al.* (1997) retained *Tetragonula* as a separate but "informal" group in recognition of the following features: (1) the conspicuously projecting scutellum of workers and males; (2) the simple oviposition behavior (Sakagami *et al.* 1990); and (3) the conspicuous "success" of the group, as measured by number of species and their abundance compared to other species.

Of the various species groups that are currently recognized within *Trigona*, those within *Tetragonula* and especially the *laeviceps* group are of relevance to the present study. The following grouping of species reflects Sakagami (1978).

Table 2 Taxa present in stingless bee samples from the Thong Pha Phum District, Kanchanaburi Province, Thailand during 2004-2006.

Genus	Subgenus	Scientific name
<i>Lisotrigona</i>		<i>Lisotrigona cacciae</i> (Nurse)
<i>Pariotrigona</i>		<i>Pariotrigona pendleburyi</i> Schwarz
<i>Trigona</i>	<i>Lepidotrigona</i>	<i>Trigona ventralis</i> Smith <i>T. terminata</i> Smith
	<i>Lophotrigona</i>	<i>T. canifrons</i> Smith
	<i>Geniotrigona</i>	<i>T. thoracica</i> Smith
	<i>Tetrigona</i>	<i>T. apicalis</i> Smith <i>T. melanoleuca</i> Cockerell
	<i>Tetratrigonula</i>	<i>T. atripes</i> Smith <i>T. collina</i> Smith <i>T. pagdeni</i> Schwarz <i>T. fuscobalteata</i> Cameron <i>T. melina</i> Gribodo <i>T. sirindhornae</i> Michener&Boongird <i>Trigona</i> sp. 1

Stingless bees morphological characters

The following descriptions of stingless bee species, which were found in the study sites, are based on the descriptive sections and keys to species of Schwarz (1939) and Sakagami (1985). In each case, the descriptions are composites and include observations based upon the series of individuals before me. The descriptions are based on bees that were attracted to honey baits and thus only workers are described. Individual bees were all fully pigmented adults.

A preliminary key to species is provided in Appendix A.

***Lisotrigona cacciae* (Nurse) (Figure 11)**

- Melipona cacciae* Nurse, 1907. Jour. Bombay Nat. Hist., 50c. 17: 619.
- Trigona scintillans* Cockerell, 1920. Annals and Mag. Nat. Hist., 9 (5): 116.
- Trigona scintillans* Cockerell, 1920. Philippine Jour. Sci., 17: 228.
- Trigona scintillans* Cockerell, 1929. Annals and Mag. Nat. Hist., 10 (6): 590.
- Trigona scintillans* Cockerell: Schwarz, 1937. Bull. Amer. Mus. Nat. Hist., 73: 327.
- Trigona scintillans* Cockerell: Schwarz, 1939. Bull. Amer. Mus. Nat. Hist., 76: 130.
- Lisotrigona (Hypotrigona) scintillans* (Cockerell): Sakagami and Yoshikawa, 1961, Nature and Life in Southeast Asia, 1: 440.
- Lisotrigona cacciae* (Nurse): 1961, Moure, Studia Entomol., 4: 194.
- Lisotrigona scintillans* (Cockerell): 1961, Moure, Studia Entomol., 4: 195.
- Hypotrigona (Lisotrigona) scintillans* (Cockerell): Sakagami 1975. Jour. Pac. Sci., 6 (20): 51.
- Lisotrigona cacciae* (Nurse): Engel, 2000, Oriental Insects, 34: 230.

Material examined: 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Diagnosis: This is the type species for the genus. It is most similar to *L. furva* but has brown integument (coal-black in all *L. furva*), and lacks pubescence on the hypoepimeron (present in *L. furva*). The following description is a composite based upon the series of individuals before me.

Description of worker

Measurements:	Total body length 3.50 - 3.64 mm
	Fore wing length 2.73 - 3.40 mm
	Head width 1.25 - 1.50 mm
	Head length 1.13 - 1.33 mm
	Scape length 0.48 - 0.58 mm
	Hind tibia length 1.60 - 1.69 mm
	Hind tibia width 0.51 - 0.56 mm

Color

Head dark brown and shining. Clypeus and supraclypeal area dull pale yellow. Mandible yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape yellow except apical quarter sometimes brown; pedicel and flagellum light brown. Mesosoma dark brown and shining and brown on tegula. Wing veins pale yellow to light brown; membrane hyaline. Mesoscutum and mesoscutellum black and shining. Legs brown except yellow on trochanters, tarsi exclusive of basitarsi, and on lateral, inner and apical borders of meso- and metabasitarsus. Metasoma light to dark brown.

Pubescence: Hairs generally silvery or white. Face uniformly sparsely pubescent. Clypeus with minute, silvery, simple hairs scattered over surface. Mesopleuron and metapleuron sparsely hairy posteriorly. Hair fringing hind tibiae posteriorly simple not branched.

Morphology

Head and mesoscutal punctures sparser and interspaces lustrous. Malar space distinctly narrower than width of flagellomere 2. Mesoscutellum short and not extended backward to over-roof the propodeum.

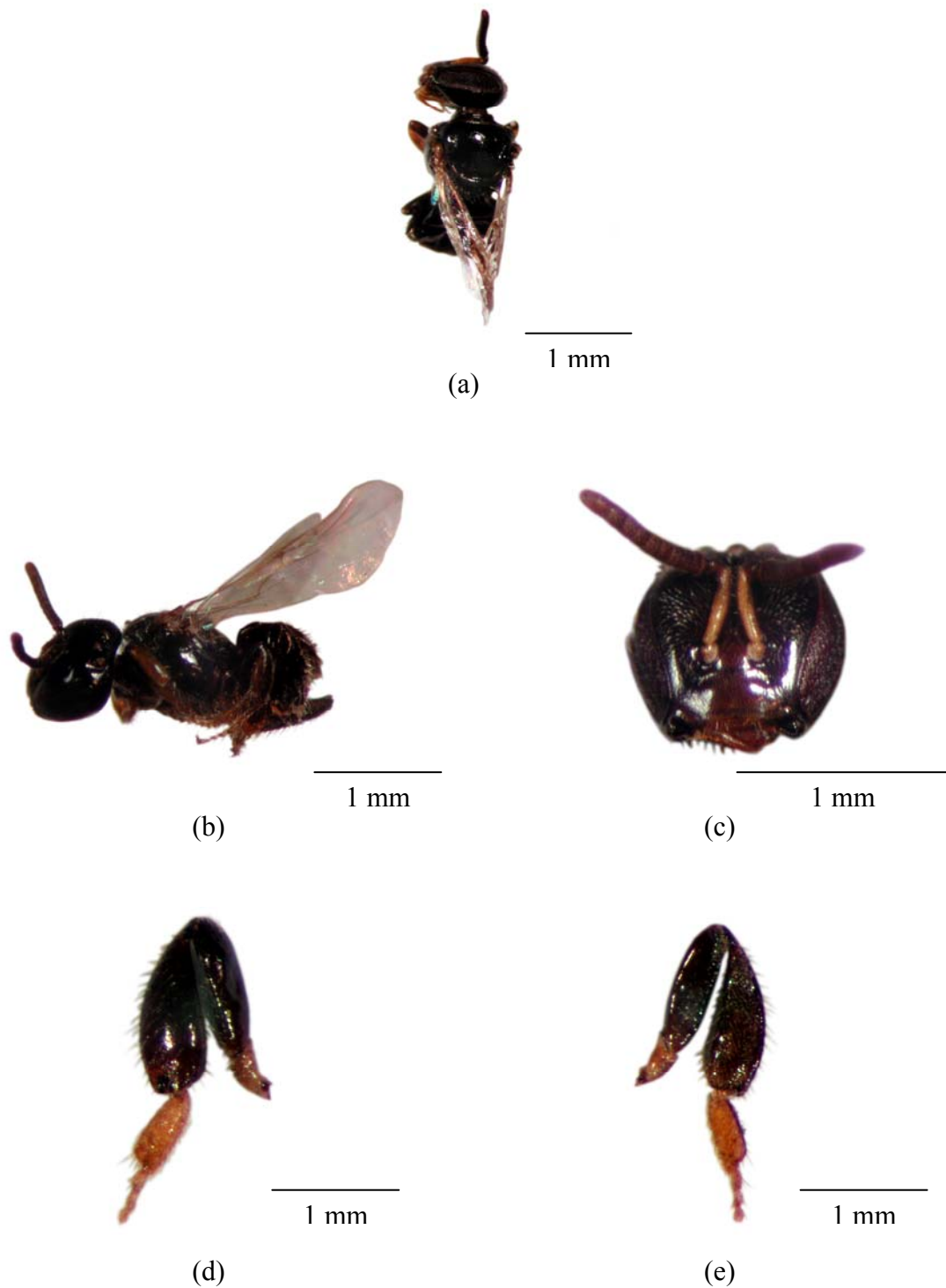


Figure 11 *Lisotrigona cacciae* (Nurse)

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Pariotrigona pendleburyi* Schwarz (Figure 12)**

Trigona pendleburyi Cockerell: Schwarz, 1939. Bull. Amer. Mus. Nat. Hist., 76: 327.

Lisotrigona pendleburyi (Nurse): Moure, 1961. Studia Entomol., 4: 194.

Lisotrigona pendleburyi (Cockerell): Moure, 1961. Studia Entomol., 4: 195.

Hypotrigona (Lisotrigona) pendleburyi (Cockerell): 1975. Jour. Pac. Sci., 4(20):
49 - 76.

Pariotrigona Pendleburyi Schwarz; 2000. Bee of the world.

Material examined: 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Note: This species has recently been placed in *Lisotrigona*, which has been regarded as either a separate genus or a subgenus of *Hypotrigona*. Professor Charles Michener, University of Kansas, has examined material of *pendleburyi* collected during the present study and is of the opinion that the species is best placed in the genus *Pariotrigona* (Michener, pers. comm.).

Description of worker

Measurements: Total body length 2.90 - 3.20 mm
Fore wing length 3.10 - 3.31 mm
Head width 1.35 - 1.53 mm
Head length 1.25 - 1.33 mm
Scape length 0.50 - 0.56 mm
Hind tibia length 0.50 - 0.61 mm
Hind tibia width 0.25 - 0.31 mm

Color

Head dark brown. Clypeus and supraclypeal area dull yellow. Mandible yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape yellow; pedicel and flagellum reddish brown. Mesosoma black and shining, except light brown on tegula. Wing veins pale yellow to light brown; membrane hyaline. Mesoscutum black and shining. Mesoscutellum pale yellow. Legs light brown except tarsi black and apical quarter light brown and on lateral, inner and apical borders of mesobasitarsus and metabasitarsus. Metasoma light brown to brown.

Pubescence: Hairs generally silvery or white. Face more densely pubescent over lower portion than over upper portion. Clypeus with minute, silvery, simple hairs scattered over surface. Mesopleuron and metapleuron sparsely hairy posteriorly. Hair fringing hind tibiae posteriorly simple, not branched.

Morphology

Head and mesosoma finely and distinctly punctate, interspaces dimly shining. Malar space distinctly wider than width of flagellomere 2. Mesoscutellum short, not extended backward to over-roof the propodeum.

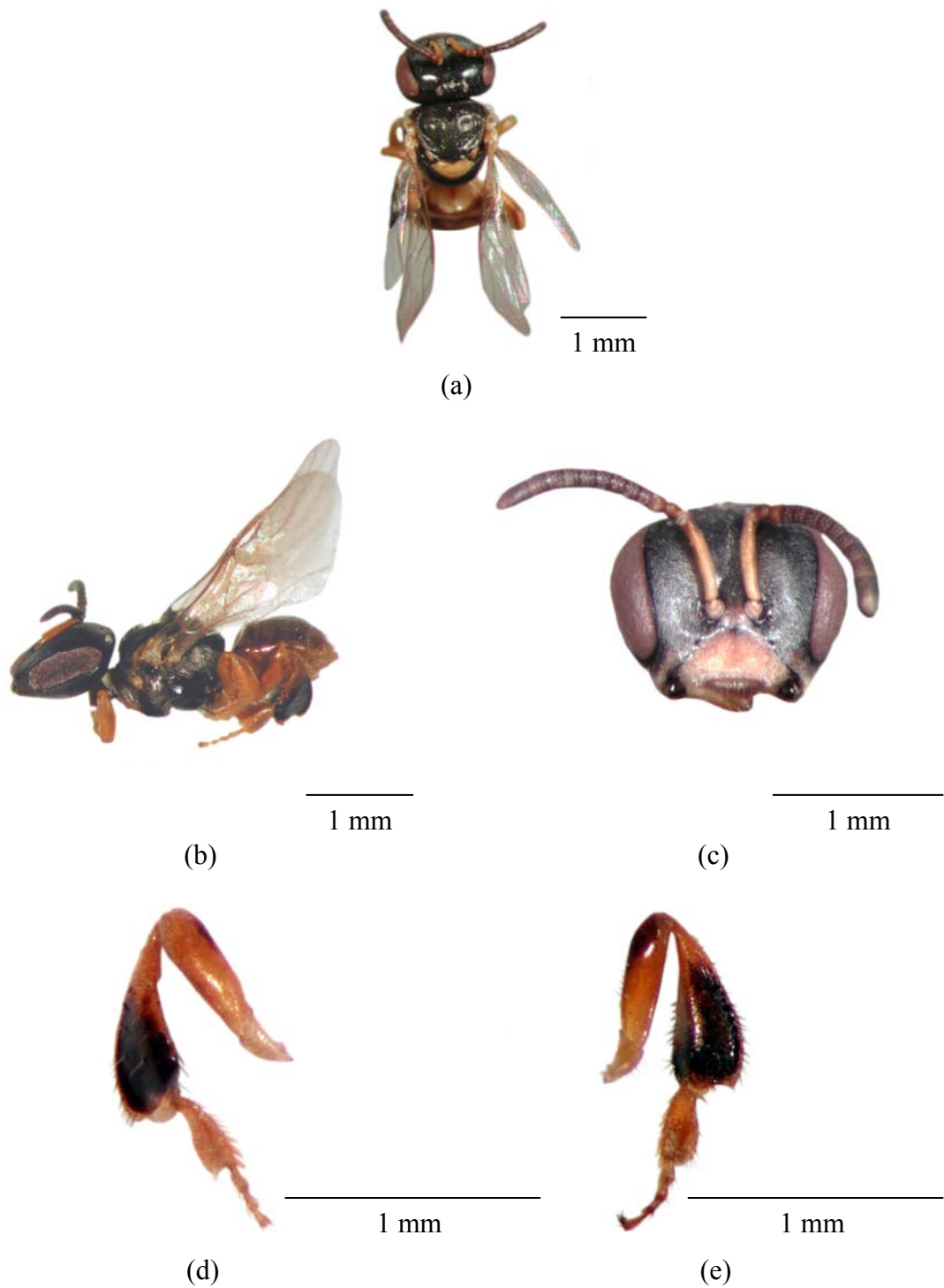


Figure 12 *Pariotrigona pendleburyi* Schwarz

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Lepidotrigona) ventralis* Smith (Figure 13)**

Trigona ventralis Smith, 1857. Journ. Proc. Linn. Soc. Zool., 2: 50.

Trigona ventralis Smith, 1871. Journ. Proc. Linn. Soc. Zool., 6: 395.

Melipona ventralis Dalla Torre, 1896. Catalogus Hymenopterorum, 10: 562 - 563.

Trigona ventralis Cockerell, 1923. Annals and Mag. Nat. Hist., 9(12): 241.

Trigona ventralis Schwarz, 1939. Bull. Amer. Mus. Nat. Hist., 76: 282 - 326.

Material examined 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Measurements:

- Total body length 4.00 - 4.20 mm
- Fore wing length 4.40 - 4.50 mm
- Head length 1.71 - 1.82 mm
- Head width 2.0 - 2.10 mm
- Scape length 0.55 - 0.73 mm
- Hind tibia length 1.71 - 1.75 mm
- Hind tibia width 0.53 - 0.62 mm

Color

Head dark brown. Clypeus and supraclypeal area dark brown. Mandible brown except apical margin and base dark brown. Labrum and other mouthparts brown. Scape dark brown except apical quarter sometimes brown; pedicel and flagellum dark brown. Mesosoma dark brown and light brown on tegula. Wing veins light brown; Wings hyaline and iridescent. Mesoscutum and mesoscutellum dark. Metasoma light to dark brown and usually a black spot on each side of the otherwise pale tergite 1 of abdomen. Legs brown except light brown on trochanters.

Pubescence: Hairs generally cinereous. Face uniformly densely and more densely pubescent over lower portion than over upper portion. Clypeus with minute,

silvery, simple hairs scattered over surface. Mesoscutum enclosed by a boarder of short thick scale-like or tomentose yellowish hairs. Mesopleuron and metapleuron sparsely hairy posteriorly. Hairs fringing hind tibiae posteriorly feathery or finely branched.

Morphology

Hind tibiae one-third as wide toward the apex as long.

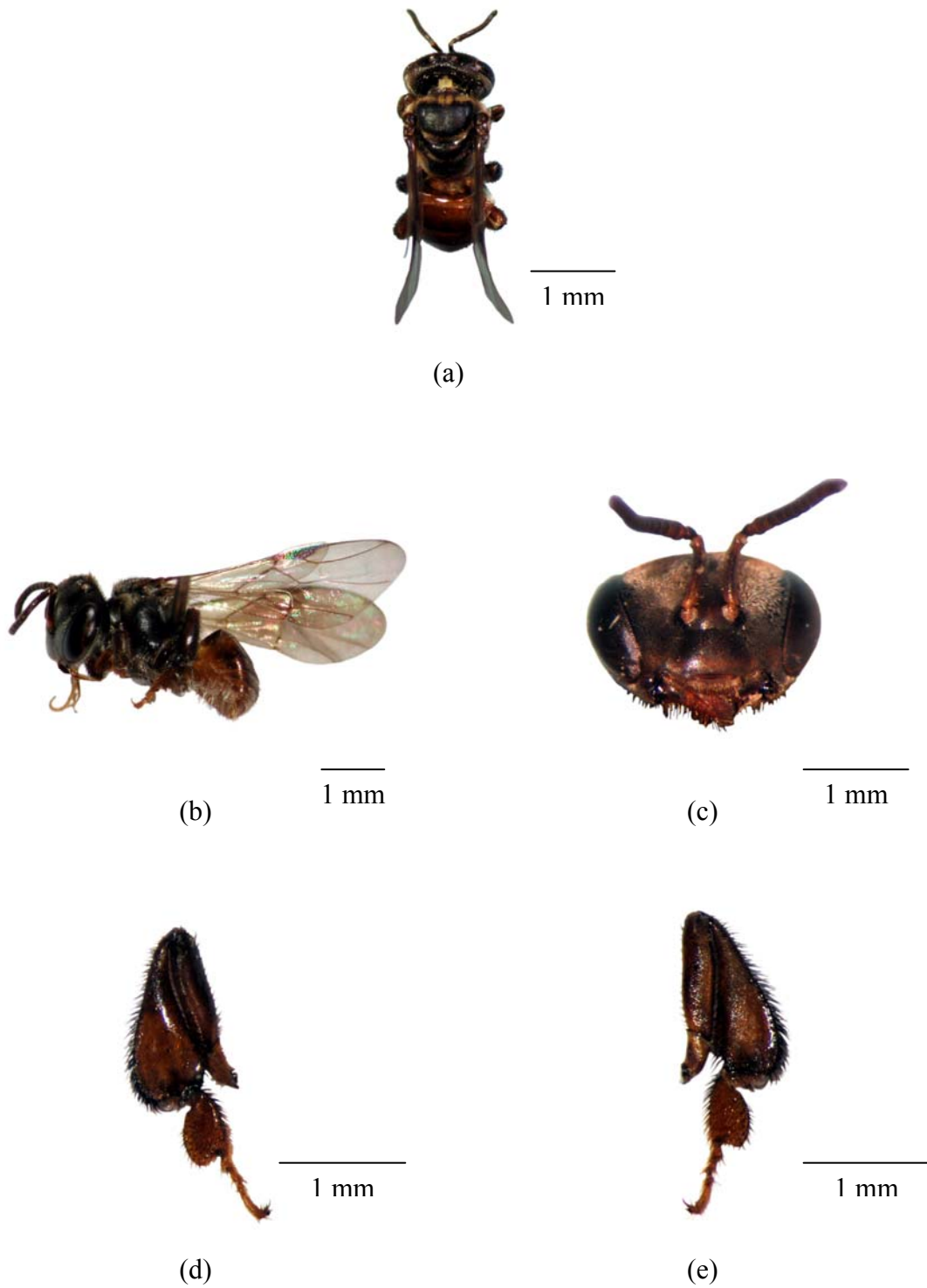


Figure 13 *Trigona ventralis* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Lepidotrigona) terminata* Smith (Figure 14)**

Trigona terminata Smith, 1878. Journ. Asiatic Soc. Bengal, 107: 169.

Melipona terminata Dalla Torre, 1896. Catalogus Hymenopterorum, 10: 562 - 563.

Melipona ventralis form *terminata* Bingham, 1897. Fauna of British India -
Hymenoptera, 1: 563.

Trigona fulvomarginata Cockerell, 1924. Annals and Mag. Nat. Hist., 10 (4): 591.

Trigona terminata Schwarz, 1937. Bull. Amer. Mus. Nat. Hist. 73: 295 - 296.

Trigona fulvomarginata Schwarz, 1937. Bull. Amer. Mus. Nat. Hist. 73: 295 - 296.

Material examined. 20 workers, Thong PhaPhum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Measurements	Total body length 5.55 - 5.71 mm
	Fore wing length 4.80 - 5.15 mm
	Head width 2.20 - 2.33 mm
	Head length 1.75 - 1.95 mm
	Scape length 0.70 - 0.80 mm
	Hind tibia length 1.91 - 2.20 mm
	Hind tibia width 0.60 - 0.70 mm

Color

Head dark. Clypeus and supraclypeal area brown and the apex of the clypeus with fulvous transverse band. Mandible brown except apically and basally dark brown. Labrum and other mouthparts yellow. Scape yellow except apical quarter sometimes brown; pedicel and flagellum dark brown. Mesosoma dark brown except light brown (ferruginous) on tegula. Wing veins dull brown; wings hyaline and iridescent. Mesoscutellum dark. Legs extensively blackened, with fore and middle femora to some extent, fore and middle tibiae and their metatarsi to a greater extent

and hind legs black. Metasoma light to dark brown, the basal tergites partly fulvous to ivory - colored.

Pubescence: Hairs generally silvery-grey. Face uniformly densely and more densely pubescent over lower portion than over upper portion. Clypeus with minute, silvery, simple hairs scattered over surface. Mesoscutum enclosed by a boarder of short thick scale-like or tomentose yellowish hairs. Mesopleuron and metapleuron sparsely hairy posteriorly.

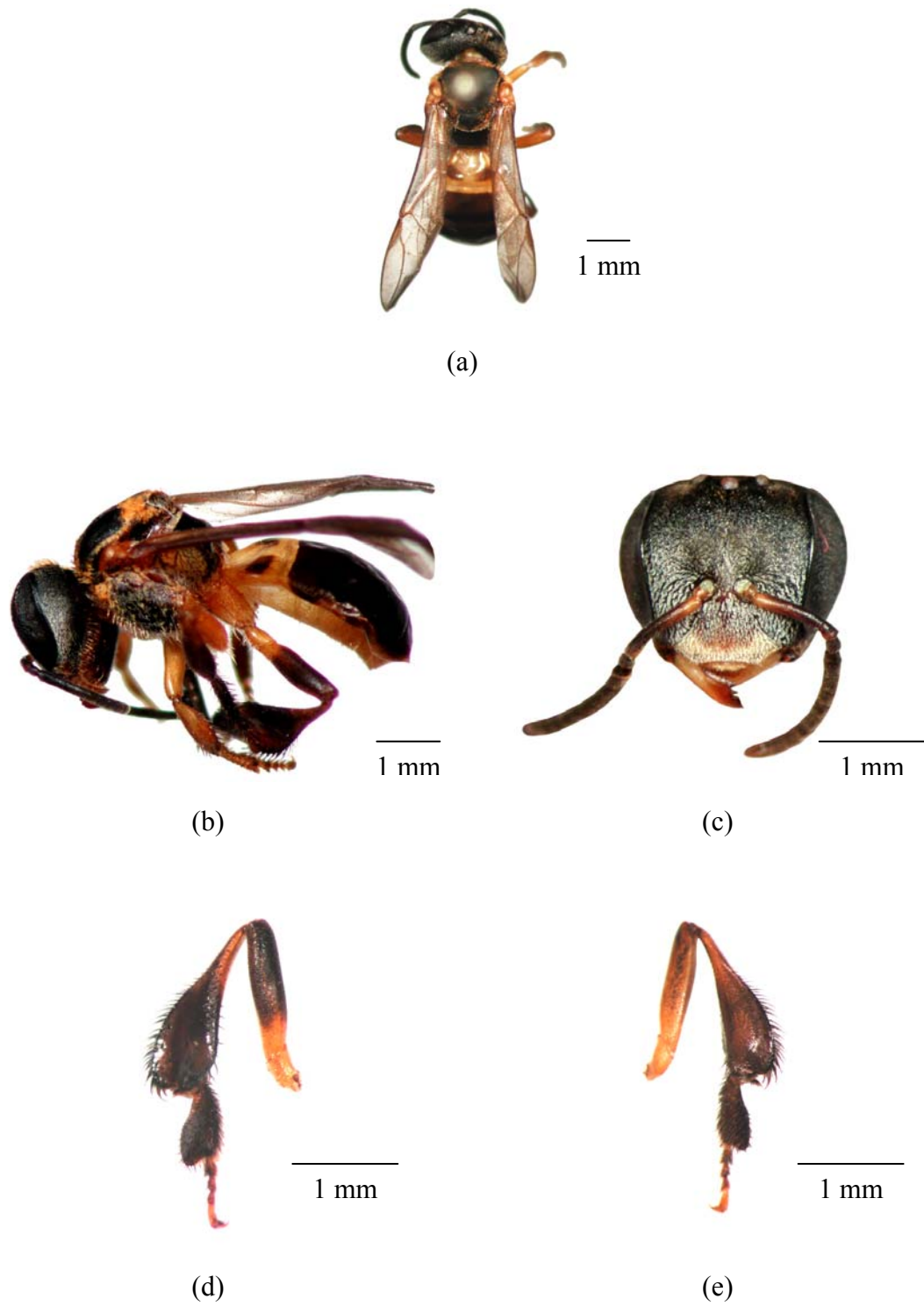


Figure 14 *Trigona terminata* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Lophotrigona) canifrons* Smith (Figure 15)**

- Trigona canifrons* Smith, 1857. Journ. Proc. Linn. Soc., Zool., 2: 51.
Trigona canifrons Smith, 1871. Journ. Proc. Linn. Soc., Zool., 11: 395.
Melipona canifrons Dalla Torre, 1896. Catalogus Hymenopterorum, 1: 576.
Melipona canifrons Bingham, 1897. Fauna of British India-Hymenoptera,
 1:560 - 562.
Trigona canifrons Cameron, 1908. Entomologist, 41: 192 -194.
Trigona busra Cockerell, 1918. Annual and Mag. Nat. Hist., 9 (2): 387.
Trigona busra Cockerell, 1919. Philippine Jour. Sci., 95: 78 -79.
Trigona busra Cockerell, 1920. Philippine Jour. Sci., 17: 228.
Trigona canifrons Cockerell, 1923. Annual and Mag. Nat. Hist., 9 (12): 241- 242
Trigona canifrons Dover, 1929. Bul. Raffles Mus., 2: 62.
Trigona canifrons Friese, 1933. Naturh. Maandblad, 22: 46.
Trigona canifrons Schwarz, 1937. Bul. Amer. Mus. Nat. Hist., 73: 282 - 289.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Diagnosis : Dollin *et al.* (1997) mention the “raised vertex and medially haired propodeum” as the important diagnostic features.

Measurements :

- Total body length 6.60 - 6.67 mm
- Fore wing length 7.30 - 7.61 mm
- Head width 3.25 - 3.41 mm
- Head length 2.80 - 2.81 mm
- Scape length 1.35 - 1.50 mm
- Hind tibia length 3.35 - 3.55 mm
- Hind tibia width 1.11 - 1.20 mm

Color

Head dark. Clypeus and supraclypeal area reddish. Mandible dark except apical margin reddish brown and base dark brown. Labrum and other mouthparts dark brown. Antennae piceous beneath, scape and pedicel dark, flagellum reddish. Mesosoma dark and reddish on tegula. Wings hyaline, sometimes slightly shaded with fuscous; veins testaceous. Mesoscutum and mesoscutellum dark. Legs more or less testaceous or piceous. Hind tibia, hind basitarsi black. Fore legs pale reddish yellow, mid and hind legs, jet-black, except for apical joint of tarsi. Metasoma: Abdomen highly polished and shining.

Pubescence: Head above and mesosoma, including propodeum somewhat thickly pubescent (woolly or moss like). Clypeus with minute, silvery, simple hairs scattered over surface. Hairs on face. Head, thorax and abdomen jet-black or sooty black, in certain lights face shows thin covering of cinereous pile. Mesopleuron and metapleuron densely and uniformly covered. The mesopleuron and metapleuron densely hairy posteriorly.

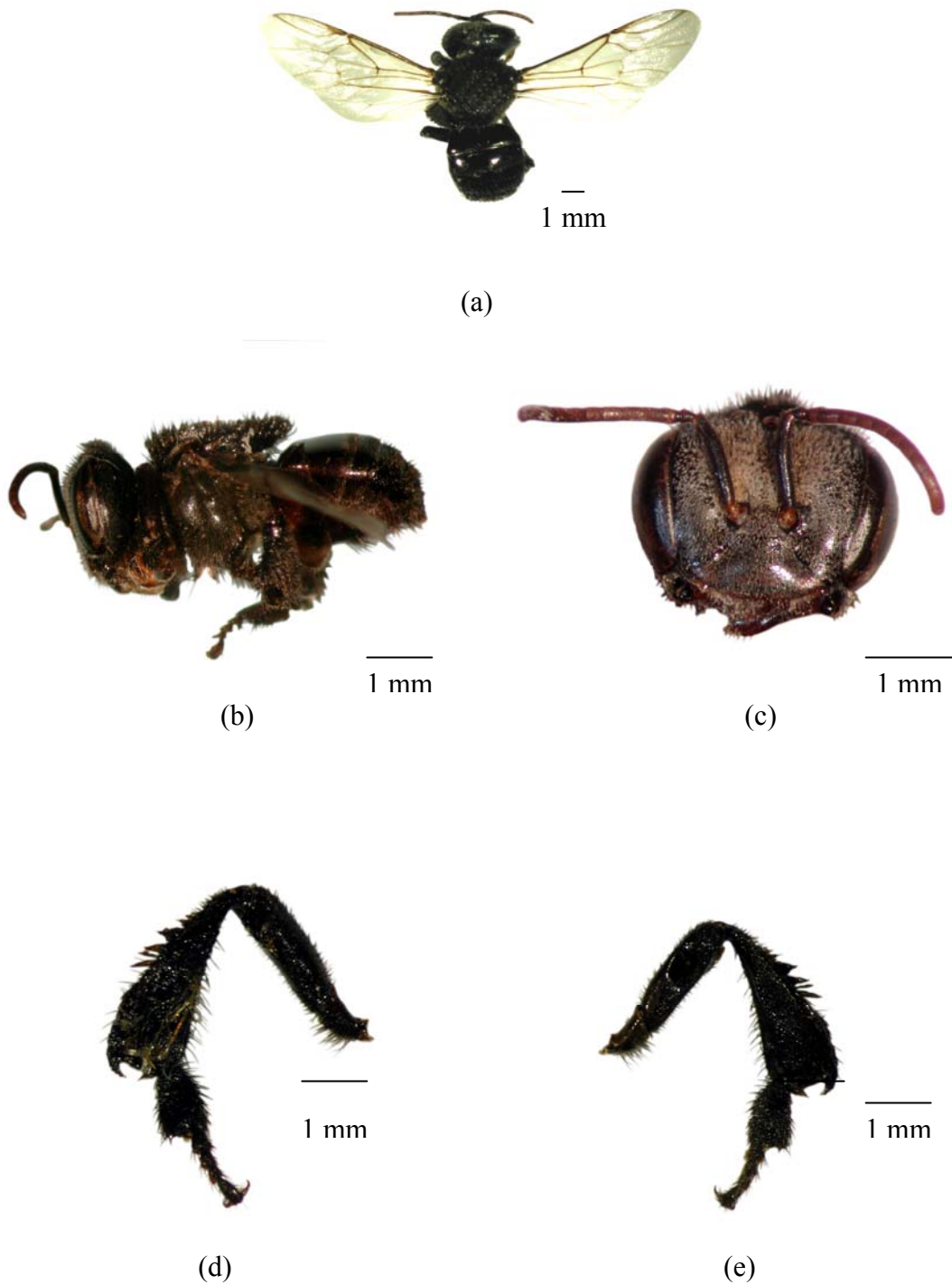


Figure 15 *Trigona canifrons* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Geniotrigona) thoracica* Smith (Figure 16)**

- Trigona thoracica* Smith, 1871. Journ. Linn. Soc., Zool., 11: 395.
Melipona thoracica Dalla Torre, 1896. Catalogus Hymenopterorum, 5: 575.
Melipona thoracica Bingham, 1897. Fauna of British India–Hymenoptera, 1: 560 - 562.
Trigona lacleifasciata Cameron, 1908. Entomological, 12: 192 - 193.
Trigona ambuala Cockerell, 1918. Annals and Mag. Nat. Hist., 9 (2): 387.
Trigona ambuala Cockerell, 1920 . Philippine Jour. Sci., 17: 228.
Trigona thoracica Cockerell, 1923. Annals and Mag. Nat. Hist., 9 (12): 241.
Trigona thoracica Dover, 1929. Bull. Raffles Mus., 2: 62.
Trigona ambuala Cockerell, 1929. Annals and Mag. Nat. Hist., 10 (4): 591.
Trigona hornatusis Friese, 1933. Naturh. Maandblad, 22: 45 - 46.
Trigona thoracica varity *lacleifasciata* Schwarz, 1937. Bul. Amer. Mus. Nat. Hist. 73: 326.
Trigona thoracica varity *ambuala* 1937. Bul. Amer. Mus. Nat. Hist., 73: 327.
Trigona thoracica varity *hornatusis* 1937. Bul. Amer. Mus. Nat. Hist., 73: 328
Trigona hemileuca Schwarz 1937. Bul. Amer. Mus. Nat. Hist., 73: 300 - 302
Trigona thoracica Schwarz, 1937. Bul. Amer. Mus. Nat. Hist., 73: 104 - 105.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Measurements	Total body length 6.91 - 7.12 mm
	Fore wing length 8.45 - 8.89 mm
	Head width 3.30 - 3.33 mm
	Head length 3.05 - 3.25 mm
	Scape length 1.35 - 1.57 mm
	Hind tibia length 3.52 - 3.70 mm
	Hind tibia width 1.25 - 1.45 mm

Color

Head dark brown. Clypeus and supraclypeal area dull pale yellow. Mandible, clypeus, and base of mandibles more or less ferruginous, the latter sometimes entirely black. Labrum and other mouthparts dark brown. Scape black, pedicel and flagellum dark brown. Mesosoma with obscurely rufo-ferruginous square mark on mesonotum. Wing flavo-hyaline and at base fusco-hyaline. Mesoscutum dark brown and with square rufo-testaceous mark. Mesoscutellum dark brown. Legs slightly ferruginous basally, but predominantly black. Metasoma black, rufo-testaceous basally.

Pubescence: Hairs generally silvery or white. Clypeus with minute, silvery, simple hairs scattered over surface. Face uniformly densely and more densely pubescent over lower portion than over upper portion. Mesopleuron and metapleuron densely hairy posteriorly.

Morphology

Hind tarsi very wide, fully two-thirds as wide as the hind tibia.

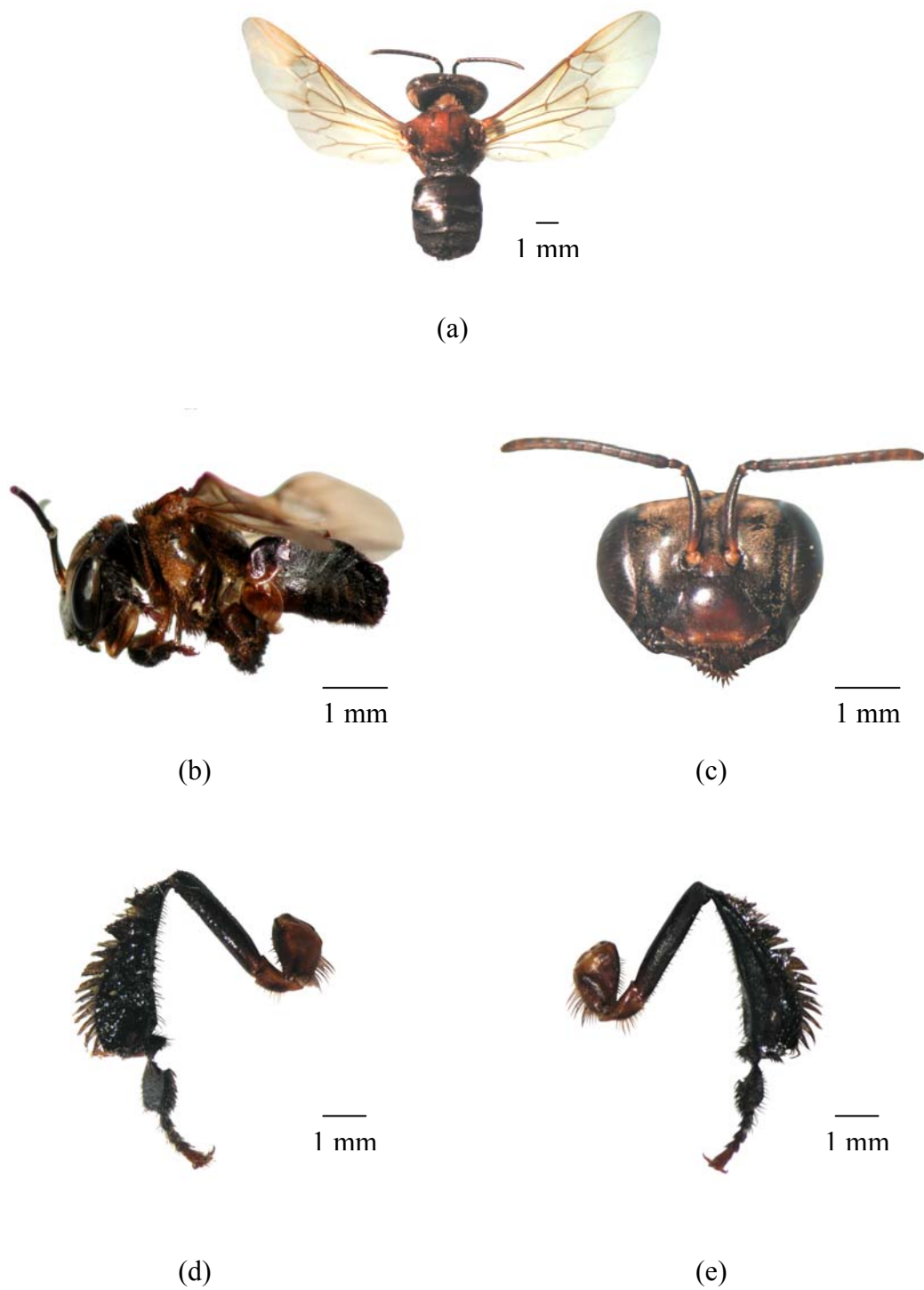


Figure 16 *Trigona thoracica* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetrigona) apicalis* Smith (Figure 17)**

- Trigona apicalis* Smith, 1857. Journ. Proc. Linn. Soc. Zool., 2: 51.
Trigona apicalis Smith, 1871. Journ. Linn. Soc. Zool., 9: 395.
Melipona apicalis Dalla Torre, 1896. Catalogus Hymenopterorum, 5: 575.
Melipona apicalis Bingham, 1897. Fauna of British India—Hymenoptera, 1: 560 - 562.
Trigona collina Waterhouse, 1903. Trans. Entom. Soc. London, 133 - 134.
Trigona apicalis Cockerell, 1918. Annals and Mag. Nat. Hist., 9 (2): 387.
Trigona apicalis Cockerell, 1920. Annals and Mag. Nat. Hist., 9 (5): 116.
Trigona apicalis Cockerell, 1920. Philippine Jour. Sci., 17: 228.
Trigona apicalis Cockerell, 1923. Annals and Mag. Nat. Hist., 9 (12): 241.
Trigona collina. Dover, 1929. Bull. Raffles Mus., 2: 62.
Trigona hemileuca Cockerell, 1929. Annals and Mag. Nat. Hist., 10 (4): 591.
Trigona apicalis. Friese, 1933. Naturh. Maandblad, 22: 45 - 46.
Trigona sericea Friese, 1933. Naturh. Maandblad, 22 45 - 46.
Trigona apicalis Schwarz, 1937. Bul. Amer. Mus. Nat. Hist., 73: 326.
Trigona sericea Schwarz, 1937. Bul. Amer. Mus. Nat. Hist., 73: 301 - 302.
Trigona hemileuca Schwarz, 1937. Bul. Amer. Mus. Nat. Hist., 73: 300 - 302.

Material examined. 20 workers, Thong Phap Pum District, Kanchanaburi Province, 9-April-2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DoA, Bangkok, Thailand.

Description of worker.

Measurements : Total body length 6.21 - 6.47 mm
 Fore wing length 8.32 - 8.40 mm
 Head width 2.65 - 2.91 mm
 Head length 2.30 - 2.45 mm
 Scape length 1.22 - 1.30 mm
 Hind tibia length 3.44 - 3.52 mm
 Hind tibia width 1.25 - 1.33 mm

Color

Head predominantly dark brown and shining. Clypeus testaceous yellow. Mandible yellow except apical margin reddish brown and base dark brown. Mouthparts and labrum generally testaceous yellow. Scape yellow except apical quarter sometimes brown; pedicel and flagellum light brown. Mesosoma dark brown and shining and brown on tegula. Wing dark brown at base, contrasting to milk-white or hyaline apical half beyond stigma of fore wing. Mesoscutum and mesoscutellum dark brown and extended backward only slightly. Legs rufo-piceous. Hind tibia, hind basitarsi and apical metasomal terga more or less darker. Metasoma usually dark, inclined to nigropiceous not infrequently suffused with red, especially on apical tergite.

Pubescence: Hairs generally silvery or white. Clypeus with minute, silvery, simple hairs scattered over surface. Mesoscutum with sparse, black, erect pubescence. Mesopleuron and metapleuron densely covered with hairs.

Morphology

Mesoscutellum extended posteriorly over propodeum.

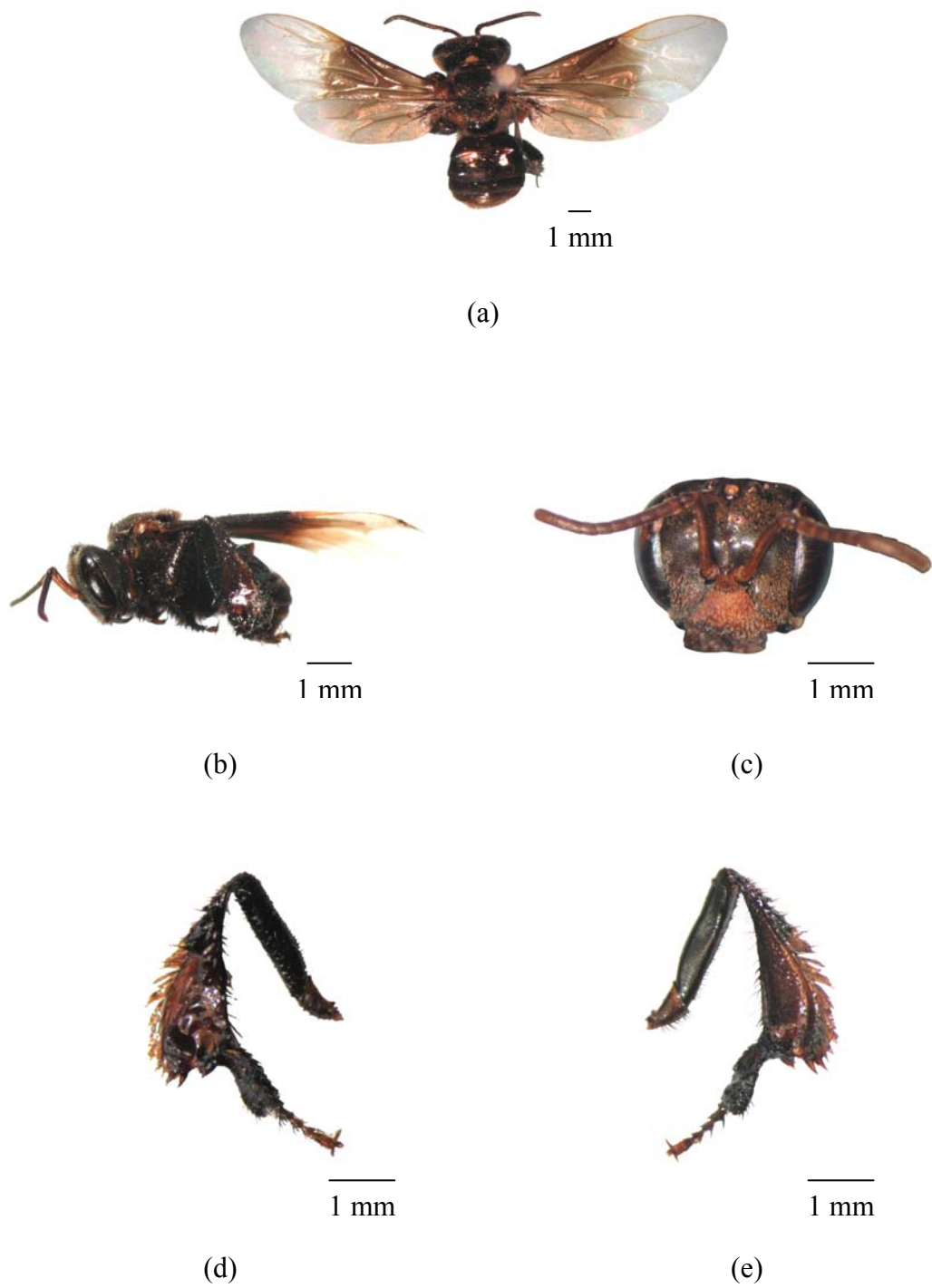


Figure 17 *Trigona apicalis* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetrigona) melanoleuca* Cockerell (Figure 18)**

Melipona vidua Lepeletier, 1836. Histoire naturelle des Insectes, Hymenopteres, 1:429.

Melipona vidua Dalla Torre, 1896. Catalogus Hymenopterorum, 5: 585.

Trigona melanoleuca Cockerell, 1929. Annals and Mag. Nat. Hist., 10 (4): 140 -141.

Trigona melanoleuca Schwarz, 1937. Bull. Amer. Mus. Nat. Hist., 73: 300 - 304.

Note.

According to the above synonymy, *vidua* Lepeletier is the oldest name for this species. However, *melanoleuca* Cockerell is the preferred name.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Description of worker

Measurements	Total body length 5.93 - 6.27 mm
	Fore wing length 6.90 - 8.00 mm
	Head width 2.61 - 2.87 mm
	Head length 2.20 - 2.35 mm
	Scape length 1.22 - 1.28 mm
	Hind tibia length 2.98 - 3.20 mm
	Hind tibia width 1.42 - 1.50 mm

Color

Head dark brown. Clypeus and supraclypeal area black except for yellowish cross band near the lower margin of the clypeus. Mandible brown except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape light brown (ferruginous), pedicel and flagellum light brown. Mesosoma dark

brown and brown on tegula. Wing dark brown at base, contrasting to milk-white or hyaline apical half beyond stigma of fore wing. Mesoscutum and mesoscutellum dark and extended backward only slightly. Legs sometimes reddish brown, with hind tibia more fulvous, sometimes with blackish clouding on coxae, trochanters, femora and middle and hind basitarsi; some specimens almost completely black. Metasoma light to dark brown.

Pubescence: Hairs generally silvery or white. Clypeus with minute, silvery, simple hairs scattered over surface. Mesopleuron and metapleuron densely hairy posteriorly.

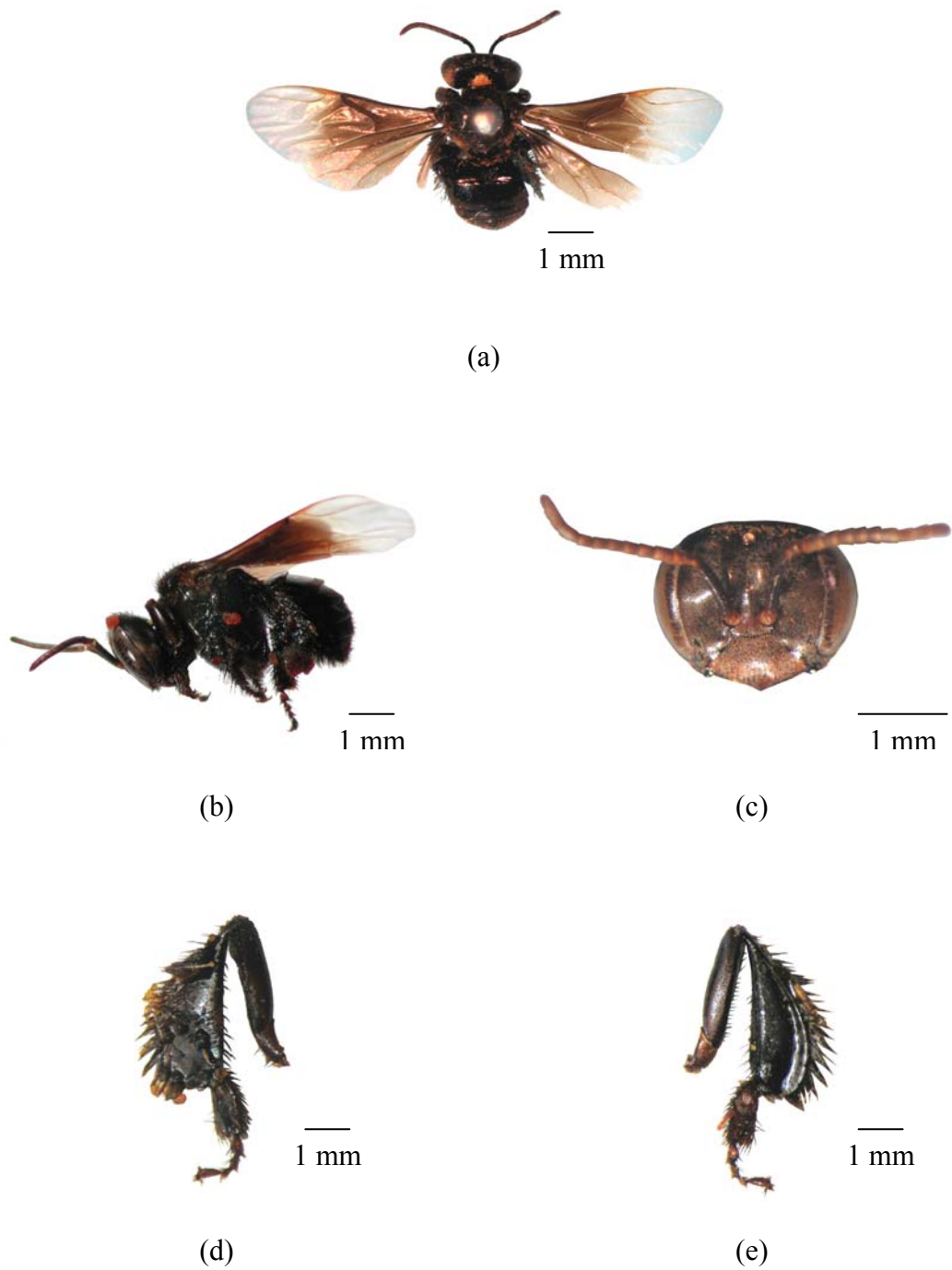


Figure 18 *Trigona melanoleuca* Cockerell

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) atripes* Smith (Figure 19)**

Trigona atripes Smith, 1857. Journ. Proc. Linn. Soc. Zool., 2: 50.

Trigona atripes Smith, 1871. Journ. Proc. Linn. Soc. Zool., 11: 395.

Melipona artipes Dalla Torre. 1896, Catalogus Hymenopterorum, 10: 576.

Melipona artipes Bingham, 1897. Fauna of British India - Hymenoptera, 1: 560 - 562.

Trigona atripes Friese, 1918. Zool. Jahrb. Syst. Geogr. U. Biol., 41: 78 -79.

Trigona atripes Cockerell, 1919. Philippine Jour. Sci., 95: 78 -79.

Trigona atripes Cockerell, 1923. Annals and Mag. Nat. Hist., 9 (12): 240.

Trigona atripes Cockerell, 1929. Annals and Mag. Nat. Hist., 9 (20): 541.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Description of worker

Measurements: Total body length 4.70 - 4.90 mm
 Fore wing length 6.33 - 6.65 mm
 Head width 2.40 - 2.42 mm
 Head length 2.10 - 2.20 mm
 Scape length 0.85 - 1.00 mm
 Hind tibia length 2.91 - 3.12 mm
 Hind tibia width 1.30 - 1.40 mm

Color

Head reddish yellow. Clypeal area yellow. Mandible brown, except apical reddish brown. Labrum and other mouthparts yellow. Scape and pedicel reddish yellow; flagellum dark brown. Mesosoma predominantly reddish to pale brown and brown on tegula. Wing reddish brown at base or over basal half, contrasting to apical half which is milk-white or hyaline beyond stigma of fore wing. Mesoscutum and

mesoscutellum reddish yellow. The mesoscutellum extended backward very emphatically. Legs more or less testaceous or piceous; fore legs pale reddish yellow; mid and hind legs jet black, except apical joints of tarsi ferruginous. Basal tergite of metasoma reddish yellow.

Pubescence: Hairs generally silvery or white. Face more densely pubescent over lower portion than over upper portion. Clypeus with minute, silvery, simple hairs scattered over surface. Mesopleuron and metapleuron sparsely hairy posteriorly.

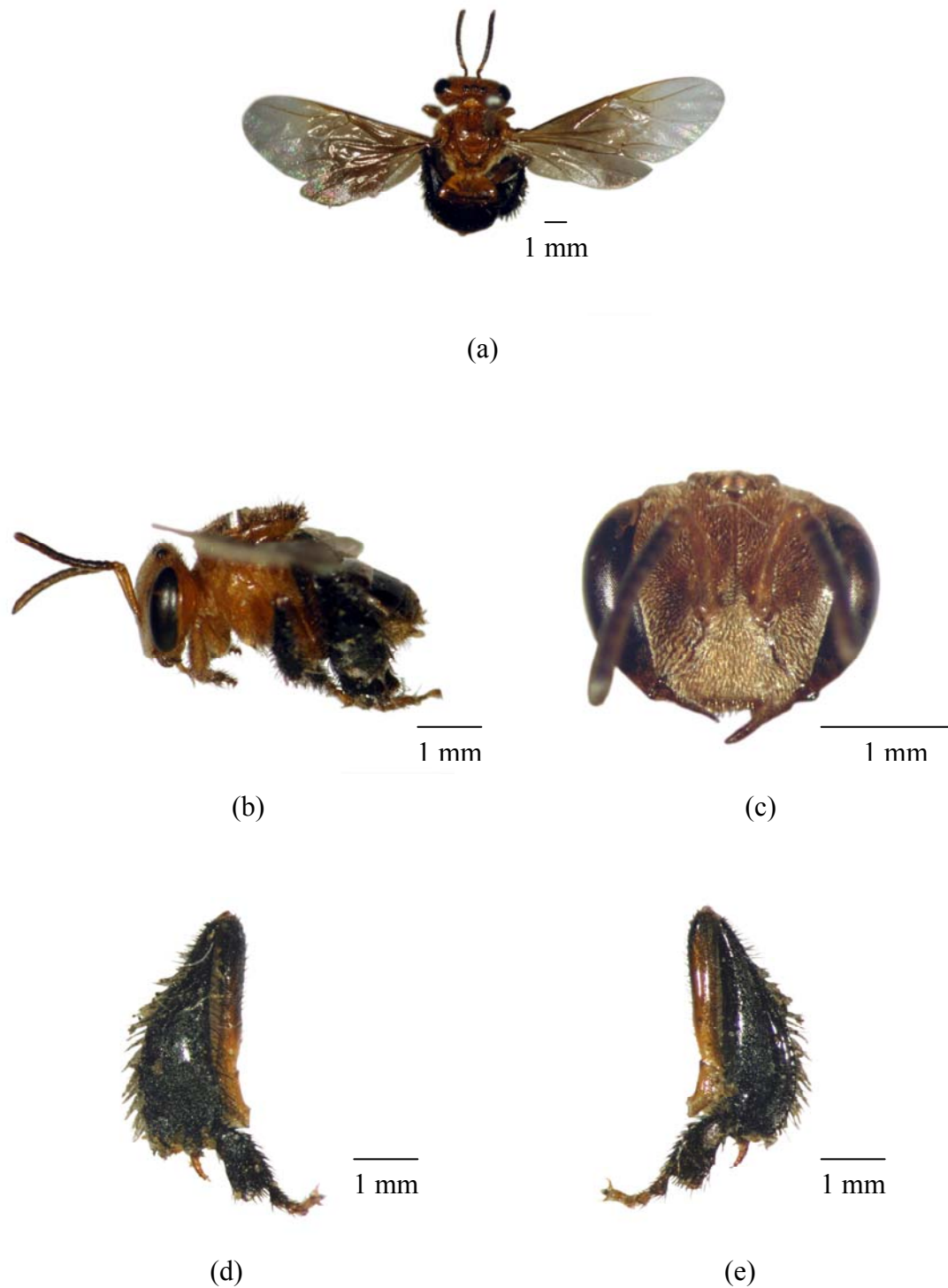


Figure 19 *Trigona atripes* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) collina* Smith (Figure 20)**

- Trigona collina* Smith, 1857. Journ. Proc. Linn. Soc. Zool., 2: 51 - 52.
Trigona collina Smith, 1858. Journ. Proc. Linn. Soc. Zool., 11: 396.
Melipona collina Dalla Torre, 1896. Catalogus Hymenopterorum, 5(10): 577.
Melipona collina Bingham, 1897. Fauna of British India – Hymenoptera, 1: 560 - 562.
Trigona collina Cameron, 1908. Entomologist, 41: 192.
Trigona collina Cockerell, 1923. Annals and Mag. Nat. Hist., 9(5): 116.
Trigona cambodiensis Cockerell, 1926. Annals and Mag. Nat. Hist., 9(44): 224.
Trigona cambodiensis Cockerell, 1929. Annals and Mag. Nat. Hist., 4: 140 - 141.
Trigona collina Schwarz, 1937. Bull. Amer. Mus. Nat. Hist., 73: 283 - 326.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Description of worker

Measurements: Total body length 5.45 - 5.71 mm
 Fore wing length 6.33 - 6.55 mm
 Head width 2.40 - 2.51 mm,
 Length 1.91 - 2.20 mm
 Scape length 1.01 - 1.21 mm
 Hind tibia length 2.66 - 3.00 mm
 Hind tibia width 1.41 - 1.50 mm

Color

Head dark brown and shining. Clypeus and supraclypeal area dull pale yellow. Face in front and clypeus black, latter with a testaceous spot. Mandible yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape and flagellum beneath rufo-testaceous. Mesosoma dark brown and

shining; black on tegula. Forewing dark brown at base, contrasting to apical half which is milk-white or hyaline beyond stigma. Mesoscutum and mesoscutellum dark. Legs: hind tibia, hind basitarsi and apical metasomal terga more or less darker. Legs more or less testaceous or piceous. Metasoma light to dark brown.

Pubescence: Head and thorax, sparsely pubescent. Head in front and clypeus with cinerous pile; a spot on the latter. Hairs generally silvery or white. Clypeus with minute, silvery, simple hairs scattered over surface. Hair fringing hind tibiae posteriorly feathery or finely branched. Mesopleuron and metapleuron densely hairy posteriorly.

Morphology Mesoscutellum extended backward very emphatically.

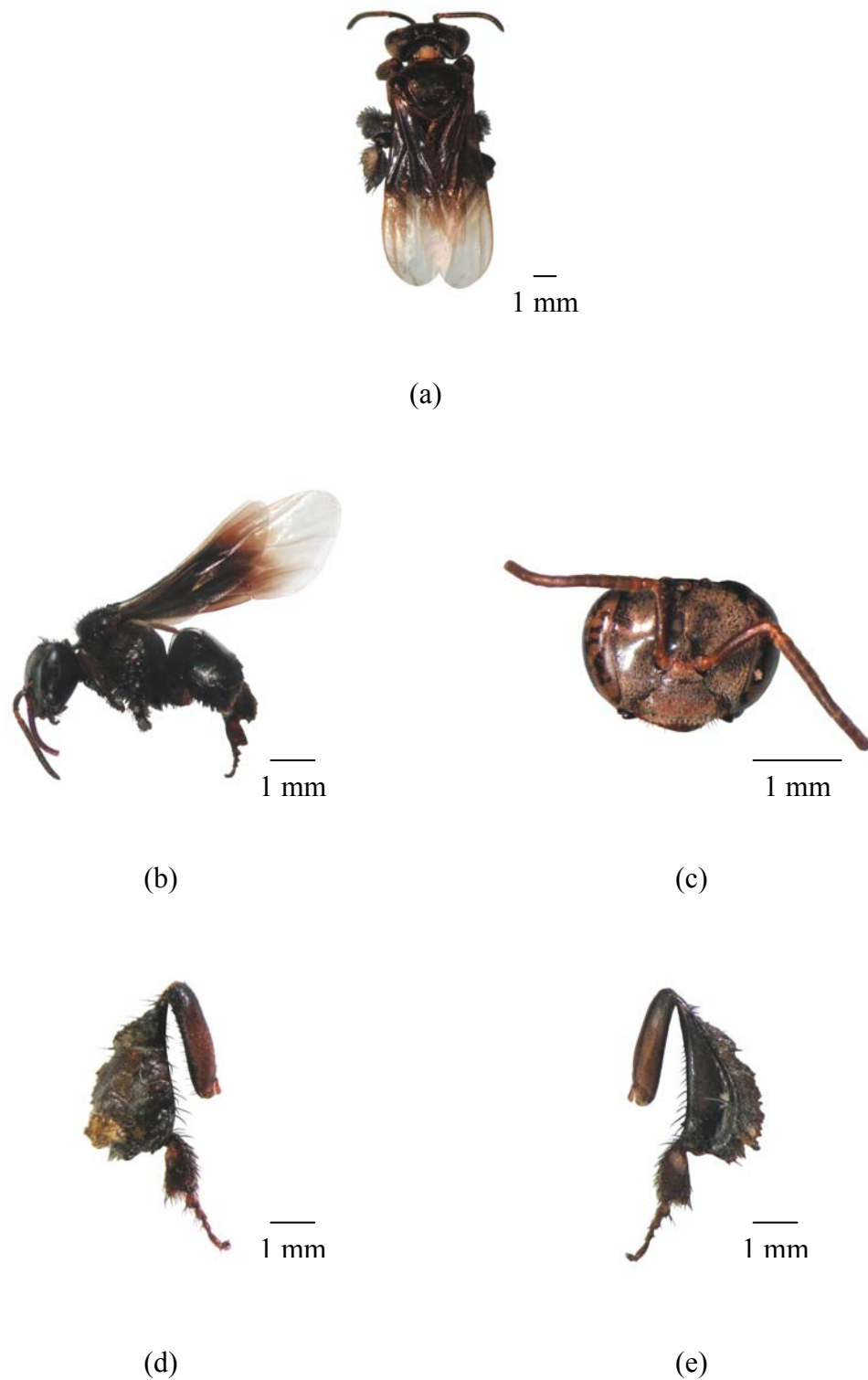


Figure 20 *Trigona collina* Smith

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) melina* Gribodo (Figure 21)**

Trigona melina Gribodo, 1893. *Bullet. Soc. Entom. Italiana.*, 25: 262 - 263.

Melipona melina Dalla Torre, 1896. *Catalogus Hymenopterorum*, 10: 580.

Trigona melina Friese, 1909. *Annals Musei Nat. Hungarici.*, 7: 272 - 276.

Trigona melina Cockerell, 1920. *Philippine Journ. Sci.*, 17: 228.

Trigona melina Schwarz, 1937. *Bul. Amer. Mus. Nat. Hist.*, 73: 283 - 316.

Tetragonula melina Moure, 1961. *Studia Entomologia (Petrópolis)*. 4: 210.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DoA, Bangkok, Thailand.

Description of worker

Measurements: Total body length 4.92 - 5.10 mm
 Fore wing length 5.20 - 5.35 mm
 Head width 2.33 - 2.45 mm
 Head length 1.92 - 2.10 mm
 Scape length 0.90 - 0.97 mm
 Hind tibia length 2.41 - 2.45 mm
 Hind tibia width 0.69 - 0.90 mm

Color

Head usually wholly honey-colored to ferruginous. Clypeus and supraclypeal area dull pale yellow. Mandible usually wholly honey-colored to ferruginous except apical dark brown. Labrum and other mouthparts yellow. Scape, flagellum as a rule dark above. Mesosoma ferruginous and brown on tegula. Wing veins light brown. Mesoscutum and mesoscutellum honey-colored to ferruginous. Legs usually wholly honey-colored to ferruginous except coxa, trochanter and femur of mid and hind leg light brown. Metasoma honey-colored to ferruginous.

Pubescence: Hairs generally silvery or white. Face uniformly densely and more densely pubescent over upper portion than over lower portion. Clypeus with minute, silvery, simple hairs scattered over surface. Mesopleuron and metapleuron sparsely hairy posteriorly.

Morphology

Flagellum conspicuously larger and more robust.

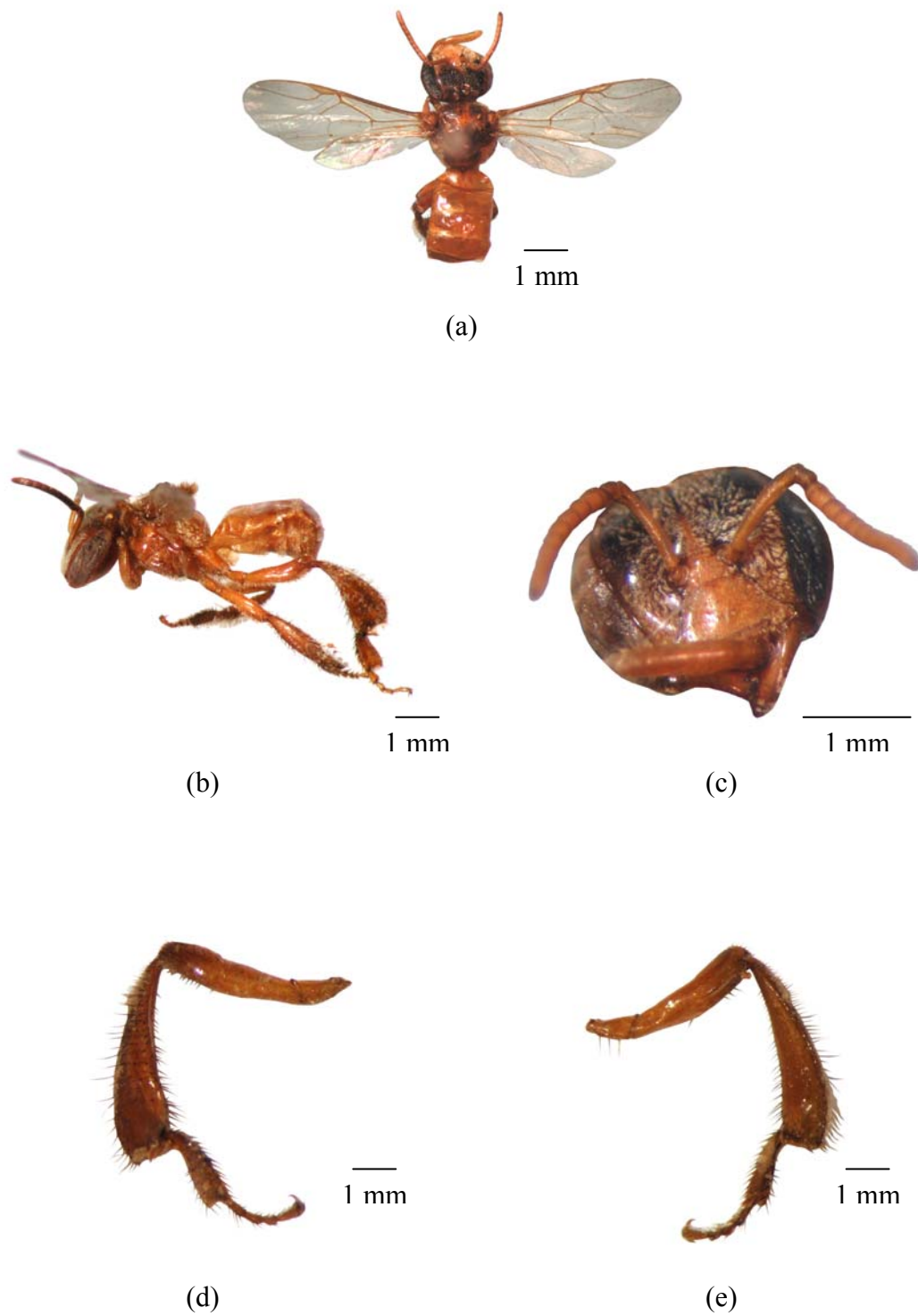


Figure 21 *Trigona melina* Griboda

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) fuscobalteata* Cameron (Figure 22)**

- Trigona ruficornis* Horne, 1870. Trans. Zool. Soc. London, 7: 185.
Trigona ruficornis Smith, 1870. Trans. Zool. Soc. London, 7: 194.
Melipona ruficornus Dalla Torre, 1896. Catalogus Hymenopterorum, 10: 583.
Melipona smithii Bingham, 1897. Fauna of British India-Hymenoptera, 1: 563.
Trigona fuscobalteata Cameron, 1908. Entomologist, 41: 192 -195.
Trigona atomella Cockerell, 1919. Annals and Mag. Nat. Hist., 9(3): 243 - 244.
Trigona atomella Cockerell, 1920. Annals and Mag. Nat. Hist., 9(5): 116.
Trigona atomella Cockerell, 1929. Annals and Mag. Nat. Hist., 10(4): 590.
Trigona pygmaea Friese, 1933. Naturh. Maandblad, 22: 147.
Melipona (Trigona) atomella Yasumatsu, 1935. Mushi, 94.
Trigona fuscobalteata : Schwarz, 1937. Bull. Amer. Mus. Nat. Hist., 73: 310 - 326.
Trigona atomella : Schwarz, 1937. Bull. Amer. Mus. Nat. Hist., 73: 310 - 328.
Trigona atomella : Cockerell, 1926. Annals and Mag. Nat. Hist., 9(19): 224.
Trigona cambodiensis Cockerell, 1939. Occas. Papers Bishop Mus., 15: 61 - 64.
Tetragonula fuscobalteata : Moure, 1961. Studia Entomologia (Petrópolis) 4: 210.

Note The oldest name for this species is *ruficornis* Horne. However, the younger name *fuscobalteata* Cameron is preferred

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Measurements :

- Total body length 2.87 - 3.25mm
- Fore wing length 2.92 - 3.00 mm
- Head width 1.01 - 1.25 mm
- Head length 1.11 - 1.15 mm
- Scape length 0.35 - 0.44 mm
- Hind tibia length 1.51 - 1.55 mm
- Hind tibia width 0.33 - 0.43 mm

Color

Head black and shining. Clypeus and supraclypeal area dull pale yellow. Mandible yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape and pedicel yellow and flagellum dark brown. Mesosoma dark and shining. Wing veins light brown; membrane hyaline. Mesoscutellum dark brown. Legs dark brown except yellow on trochanters, tarsi exclusive of basitarsi, and laterally. Color of metasoma very variable, some specimens pallid testaceous with more or less fuscous bands on tergite, some specimens sepia brown to blackish to light brown.

Pubescence: Hairs generally silvery or white. Face uniformly and more densely pubescent over lower portion than over upper portion. Mesoscutum usually streaked with longitudinal hair bands. Mesopleuron and metapleuron densely hairy posteriorly. Hairs fringing anterior contour of hind tibiae silver-gray. Hair fringing hind tibiae posteriorly feathery or finely branched.

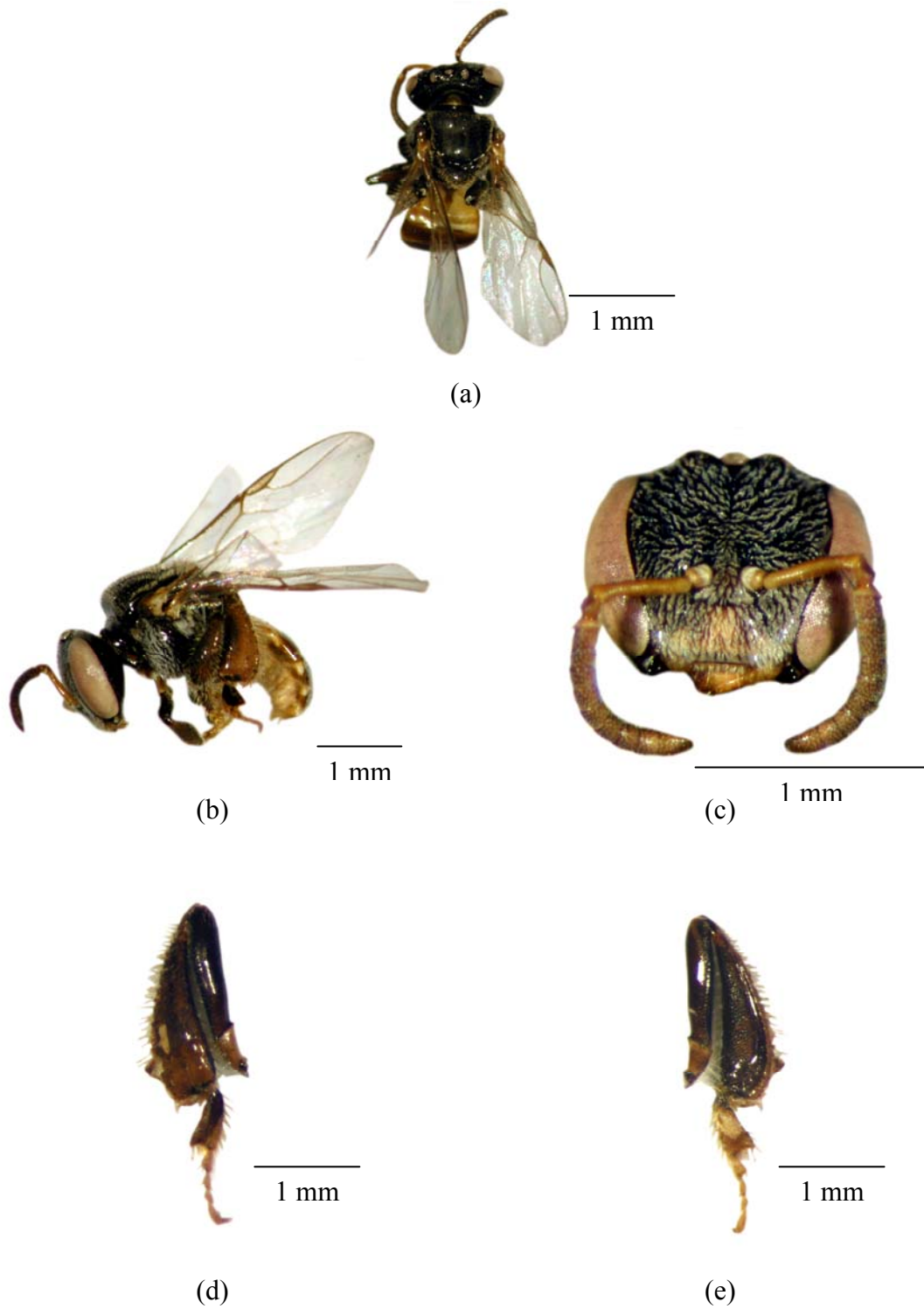


Figure 22 *Trigona fuscobalteata* Cameron

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) pagdeni* Schwarz (Figure 23)**

Trigona fascobalteata varity *pagdeni*: Schwarz, 1937. Bull. Amer. Mus. Nat. Hist.,
73: 110.

Tetragonula pagdeni : Moure, 1961. Studia Entomologia (Petrópolis) 4: 210.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Measurements: Total body length 3.84 - 4.00 mm
Fore wing length 4.55 - 4.91 mm
Head width 1.95 - 2.20 mm
Head length 1.82 - 2.17 mm
Scape length 0.68 - 0.81 mm
Hind tibia length 1.98 - 2.15 mm
Hind tibia width 0.60 - 0.65 mm

Color

Head dark brown and shining. Clypeus and supraclypeal area dark brown. Mandible dark brown except base black. Labrum and other mouthparts yellow. Scape light brown except apical quarter sometimes brown; pedicel and flagellum dark brown. Mesosoma and tegula dark brown. Wing veins dark brown; membrane hyaline. Mesoscutellum black. Legs dark brown except yellow on coxa, trochanters and tarsi. Metasoma light to dark brown.

Pubescence: Hairs generally silvery or white. Mesoscutum streaked by six longitudinal hair bands (including lateral fringes) separated from each other by five hairless areas that alternate with them. Mesopleuron and metapleuron sparsely hairy

posteriorly. Hairs fringing anterior contour of hind tibiae silver-gray to light brown. Hair fringing hind tibiae posteriorly feathery or finely branched.

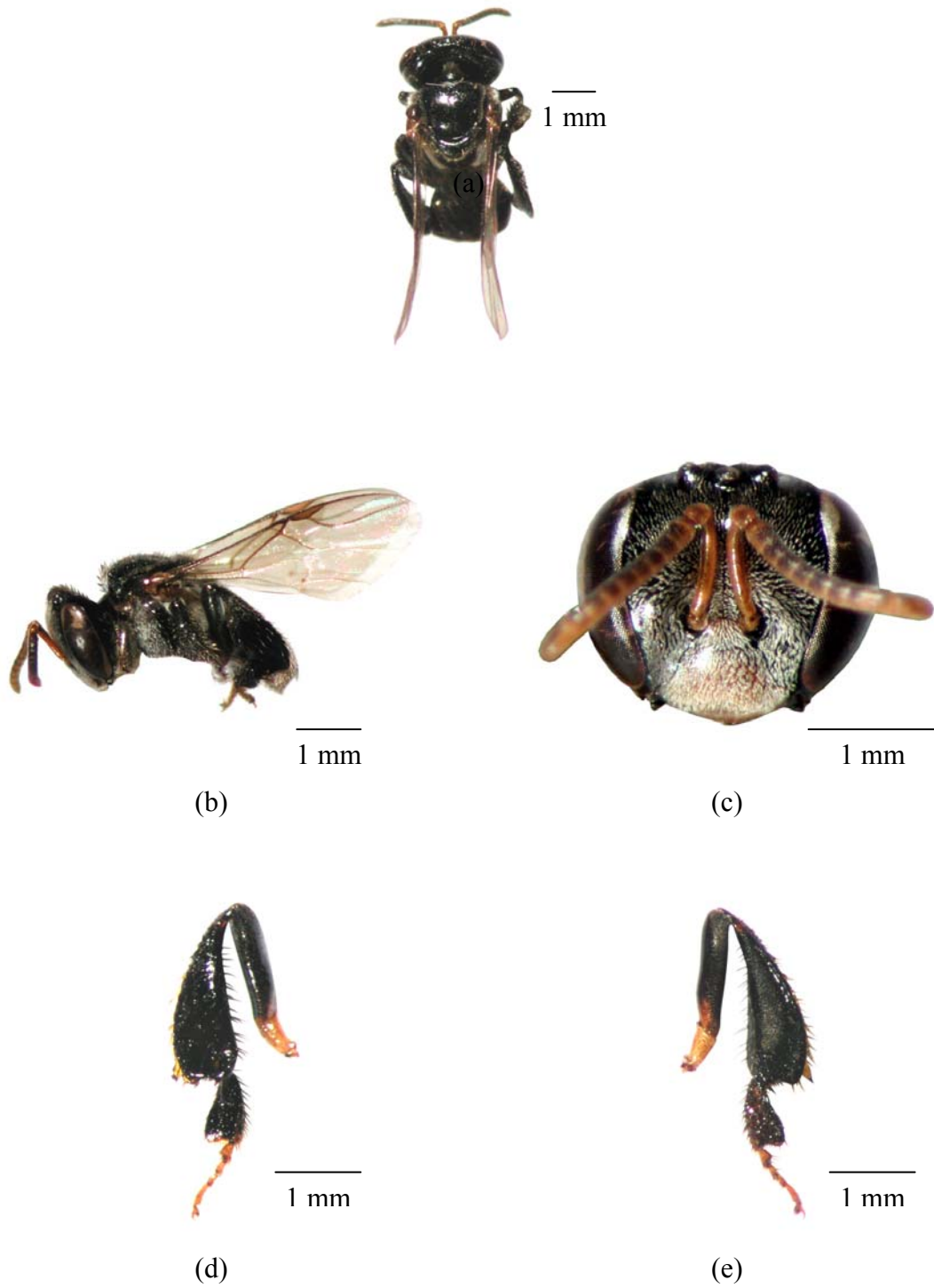


Figure 23 *Trigona pagdeni* Schwarz

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

***Trigona (Tetragonula) sirindhornae* Michener & Boongird (Figure 24)**

Trigona sirindhornae Michener & Boongird: J. of the Kansas Entom. Soc., 77(2):
143 – 146.

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Description of worker

Measurements: Total body length 3.80 - 4.10 mm
Fore wing length 4.20 - 4.66 mm
Head width 2.20 - 2.33 mm
Head length 1.69 - 1.82 mm
Scape length 0.75 - 0.85 mm
Hind tibia length 1.91 - 2.22 mm
Hind tibia width 0.57 - 0.67 mm

Color

Head black and shining. Clypeus and supraclypeal area dull pale yellow. Mandible yellowish or brownish testaceous, minutely black at apex; yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape testaceous, pedicel strongly infuscated; flagellum testaceous beneath, blackish above. Mesosoma pale yellowish brown or testaceous, except scutum black with sharply defined lateral margins narrowly reddish testaceous and brown on tegula. Mesopleuron predominantly reddish brown; scrobal pit dark brown, distinctly darker than adjacent mesopleural areas; lower third with large, black, conspicuous, anteroventral mark extending onto ventral surface of mesoma but not reaching mesopleural-metapleural suture. Metapleuron pale reddish brown. Propodeum pale, reddish brown with dense, silver pubescence. Wing slightly dusky, veins and stigma

brownish black, pale yellow to light brown; membrane hyaline. Mesoscutum black. Mesoscutellum dark brown. Legs yellowish brown or testaceous, coxae to femora about same color as most of thorax; yellow on trochanters; tibiae and tarsi darker, reddish brown; tarsi and distal parts of mid and hind tibiae sometime slightly infuscated; tarsi exclusive of basitarsi, and on latter, inner and apical borders of meso- and metabasitarsus. Metasoma light to dark brown.

Pubescence: Hairs generally silvery or white. White, appressed, plumose hairs of face well developed and largely covering surface of lower face up to slightly above level of antennal base, above that level to level of ocelli white hair progressively shorter, well-separated, inconspicuous, exposing shining surface beneath; other hairs of head and mandible testaceous or those of vertex sometime dusky. Mesopleuron and metapleuron sparsely hairy posteriorly.

Morphology

Integument largely shining and impunctate as in other species of *Tetragonula*. Scape slightly more than half as long as eye. Flagellomere 4 slightly broader than long to as broad as long, depending on curvature of flagellum.



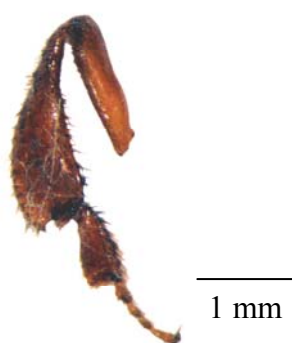
(a)



(b)



(c)



(d)



(e)

Figure 24 *Trigona sirindhornae* Michener & Boongird

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

Trigona (Tetragonula) sp. 1 (Figure 25)

Material examined. 20 workers, Thong Pha Phum District, Kanchanaburi Province, 9 April 2006, Yuvarin Boontop, pinned, deposited in Insect Museum, DOA, Bangkok, Thailand.

Description of worker

Measurements: Total body length 3.80 - 4.10 mm
 Fore wing length 4.20 - 4.66 mm
 Head width 2.20 - 2.33 mm
 Head length 1.69 - 1.82 mm
 Scape length 0.75 - 0.85 mm
 Hind tibia length 1.91 - 2.22 mm
 Hind tibia width 0.57 - 0.67 mm

Color

Head black and shining. Clypeus and supraclypeal area dull pale yellow. Mandible yellowish or brownish testaceous, minutely black at apex; yellow except apical margin reddish brown and base dark brown. Labrum and other mouthparts yellow. Scape testaceous, pedicel strongly infuscated, flagellum testaceous beneath, blackish above. Mesosoma: Thorax pale yellowish brown or testaceous, except scutum black with sharply defined lateral margins narrowly reddish testaceous and brown on tegula. Mesopleuron uniformly black. Metapleuron and propodeum both covered with silver pubescence, appearing more pale than mesopleuron. Wing slightly dusky, veins and stigma brownish black, pale yellow to light brown; membrane hyaline. Mesoscutum black, Mesoscutellum dark brown. Legs yellowish brown or testaceous, coxae to femora about same color as most of thorax; yellow on trochanters; tibiae and tarsi darker, reddish brown; tarsi and distal parts of mid and hind tibiae sometime slightly infuscated. tarsi exclusive of basitarsi, and on latter, inner, and apical borders of meso- and metabasitarsus. Metasoma light to dark brown.

Pubescence: Hairs generally silvery or white. White, appressed, plumose hairs of face well developed and largely covering surface of lower face up to slightly above level of antennal base, above that level to level of ocelli white hair progressively shorter, well-separated, inconspicuous, exposing shining surface beneath; other hairs of head and mandible testaceous or those of vertex sometime dusky. Mesopleuron and metapleuron sparsely hairy posteriorly.

Morphology

Integument largely shining and impunctate as in other species of *Tetragonula*. Scape slightly more than half as long as eye. Flagellomere 4 slightly broader than long to as broad as long, depending on curvature of flagellum.

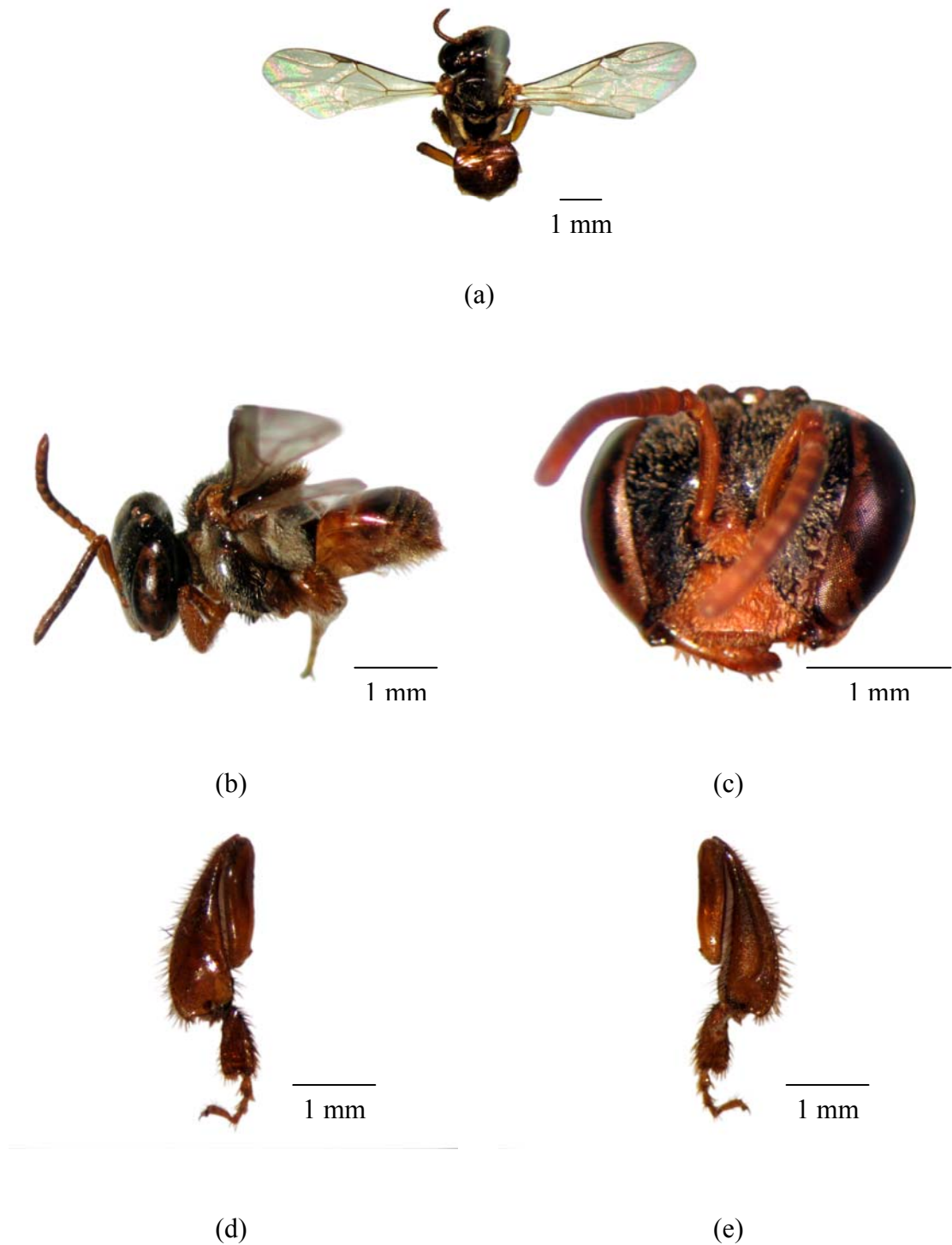


Figure 25 *Trigona* sp. 1

(a) Dorsal view

(b) Lateral view

(c) Head

(d) Outer side of hind leg

(e) Inner side of hind leg

3. Surveys of diversity of stingless bees

3.1 Species richness and abundance of stingless bee species

3.1.1 Species richness of stingless bee species

Table 3 summarized data from the honey–bait trap sampling method employed in this study. The results showed the variation in species richness and the number of individuals between the four types of forest and between the sampling seasons. Table 3 shows the following: stingless bees have their highest species richness in DDF (dry dipterocarp forest) and LMDF (lower mixed deciduous forest) (9 species), which is greater than species richness in UMDF (upper mixed deciduous forest) (7 species) and DEF (dry evergreen forest) (5 species). Abundance data revealed a slightly different ranking: the largest number of bees was obtained from DDF, UMDF, LMDF and DEF.

In order to consider temporal effects, which might affect stingless bee richness and abundance, these data were grouped according to the sampling seasons. This grouping of the data showed slight differences between sampling seasons in all forest types, as shown in Table 3.

Dry season

The dry season result showed that stingless bees were the highest species richness (9 species) in DDF and LMDF, followed by UMDF (7 species) and DEF (5 species). The largest number of bees was obtained from DDF, followed by UMDF, LMDF and DEF. The abundance of stingless bees was significantly different between the types of forest ($\chi^2 = 3,382.71$, $df = 3$, $P > 0.001$).

Wet season

The wet season result showed that stingless bees were the highest species richness (9 species) in LMDF, followed by DDF (8 species), UMDF (7 species) and DEF (5 species). The abundance rankings for the forest types were the same as in the dry season and abundance was significantly different between the types of forest ($\chi^2 = 1,768.38$, $df = 3$, $P > 0.001$).

Table 3 Species richness, number of individuals of stingless bee in four types of forest during dry and wet seasons of April 2004 to March 2005.

Type of forest	Species richness			Abundance ¹		
	All year	Dry season	Wet season	All year	Dry season	Wet season
Dry Dipterocarp forest	9	9	8	7,428	5,238	2,190
Upper Mixed Deciduous forest	7	7	7	4,079	2,985	1,094
Lower Mixed Deciduous forest	9	9	9	2,944	1,724	840
Dry Evergreen forest	5	5	5	947	676	271
Total	11	9	7	15,389	10,944	4,395

¹ Number of individuals

3.1.2 Abundance of stingless bees species

Figures 26 and 27 represent data for 11 species of stingless bees was collected by the honey-bait trap method in four types of forest during April 2004 – March 2005. The species were ranked according to their abundance. The most abundant species was found in DDF, UMDF, LMDF and DEF.

Figure 26 shows the following: stingless bees have their highest species richness and abundance in DDF and lowest in DEF. The most population was *T. ventralis* that found in DDF, UMDF and LMDF but not found in DEF. For *T. sirindhornae* and *T. collina* that found in all types of forest. And some species such as *T. canifrons* found only in DDF, *T. melina* found only in LMDF and *T. fascobalteata* found only in DEF.

Numbers of individuals

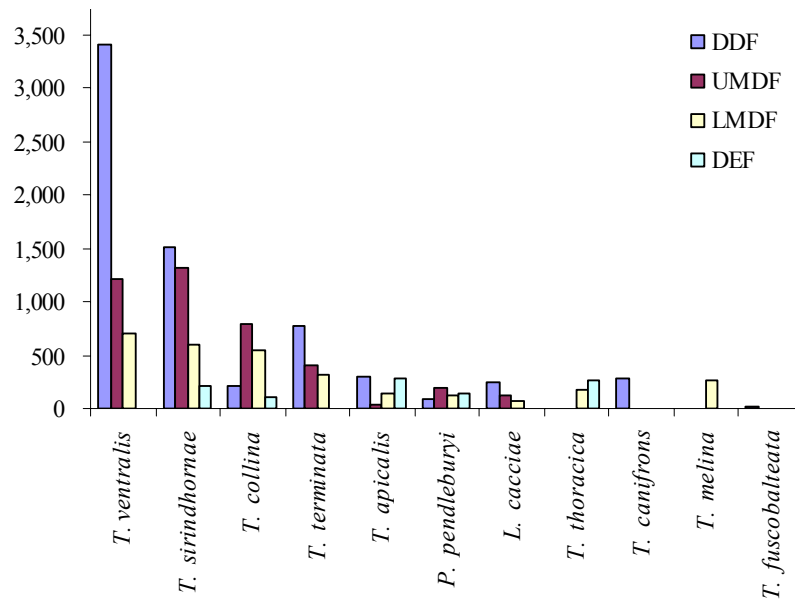


Figure 26 Species of stingless bees and their abundance (numbers of individuals) visiting honey-bait traps in four types of forest, April 2004-March 2005.

Numbers of individuals

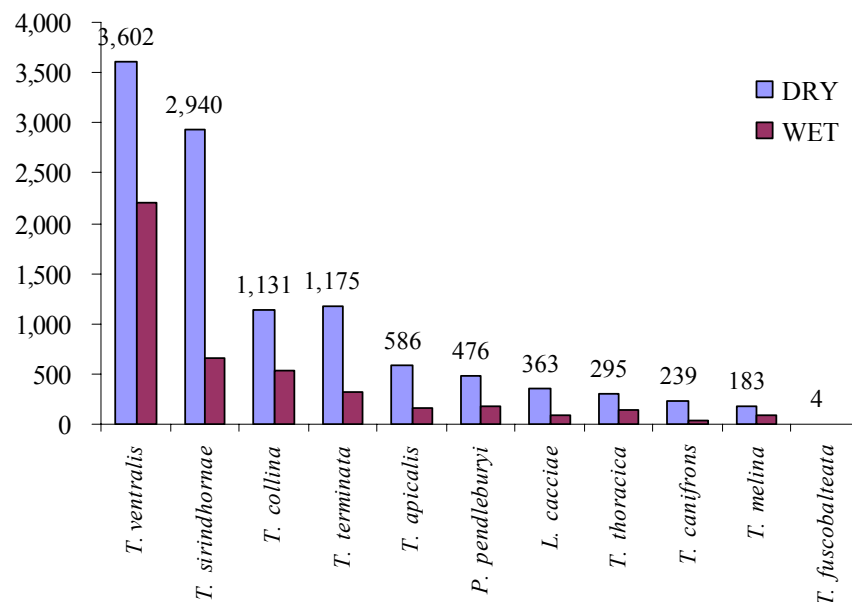


Figure 27 Species of stingless bee and their abundance (numbers of individuals) visiting honey – bait traps in four types of forest during the dry and wet seasons.

The data for species richness and abundance of stingless bees during April 2004 – March 2005 were presented in Appendix B Table 6. In order to consider the temporal effects, which might affect stingless bee richness and abundance, these data were grouped according to the sampling seasons. The grouping of these data showed clear between the sampling seasons in all forest types, as shown in Figure 27. The abundances of stingless bees in the dry and wet seasons were significantly different among the types of forest ($\chi^2 = 3382.71$, $df = 3$, $P > 0.001$ for dry season and $\chi^2 = 1768.38$, $df = 3$, $P > 0.001$ for wet season). All species were observed in both wet and dry seasons except for one species (*T. fuscobalteata*) which was observed only in the dry season from DDF (Appendix B Table 6). The total number of bees collected was 15,389 and catches ranged from just 4 individuals (*T. fuscobalteata*) to 5,813 specimens (*T. ventralis*). The data presented indicate that the dominant species was *T. ventralis* (5,813 specimens = rank no.1). The second most abundant species was *T. sirindhornae* (3,591 specimens = rank no. 2) followed by *T. collina* (1,665 specimens = rank no.3).

To examine the effect of type of forest on stingless bee abundance, these samples were grouped according to the type of forest. This new grouping of data showed little difference between types of forest, either in dry or wet seasons, as shown in Figure 28 (See also Appendix B Table 7, 8).

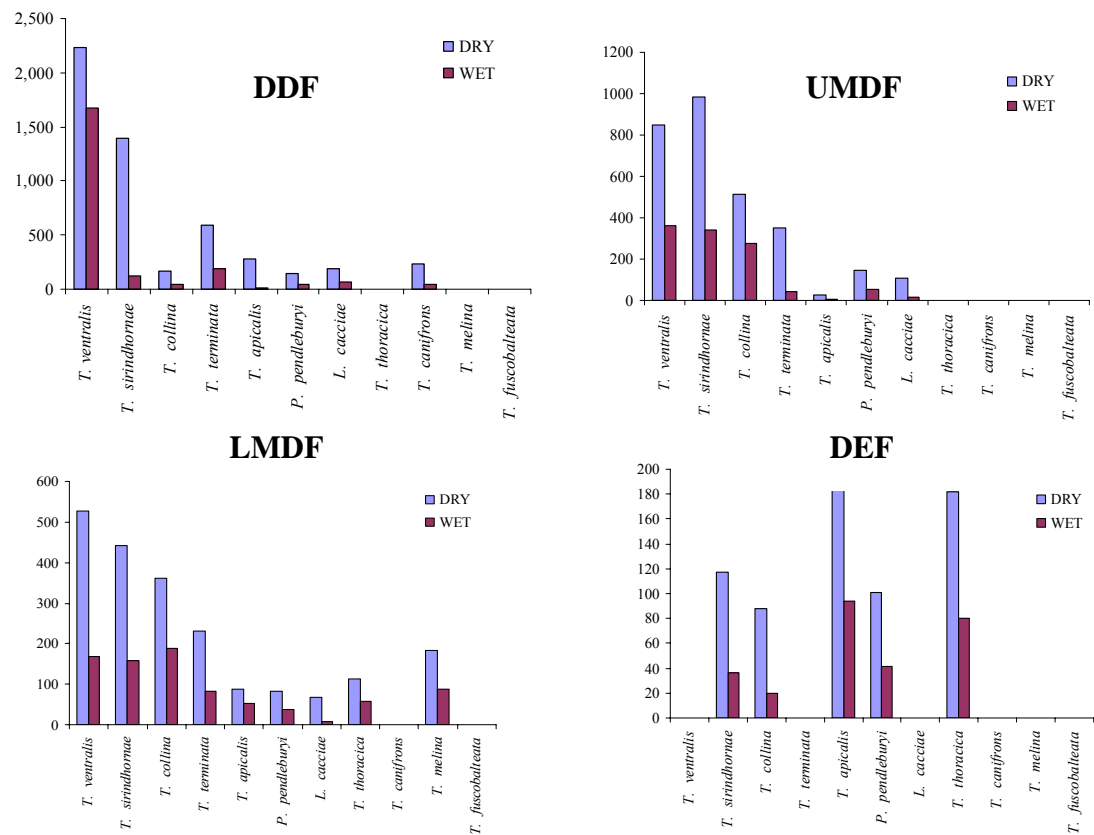


Figure 28 Species of stingless bee and their abundance visited honey-bait traps from four types of forest during the dry and wet season.

The most abundant during the sampling period was *Trigona ventralis*, *T. sirindhornae* and *T. apicalis* in DDF, U MDF, LMDF and DEF. Thus, while species richness varied only slightly between dry and wet seasons, the stingless bees were less abundances during the wet season across all forest types. All species were observed in both wet and dry seasons, except for one species (*T. fuscobalteata* = 4 specimens) which was observed only in the dry season from DDF. (Figure 28 and Appendix B Table 6)

To consider temporal effects, which might affect stingless bee richness and abundance; these data were grouped according to the sampling seasons. This grouping of data showed slight differences between sampling seasons in all forest types.

Dry season

The data for species rank and abundance of stingless bees during April 2004-March 2005 in the dry season are presented in Appendix B Table 7. The total number of bees collected was 10,994 and catches ranged from just 4 individuals (*T. fuscobalteata*) to 3,602 specimens (*T. ventralis*). The dry season data indicated that the dominant species was *T. ventralis*, followed by *T. sirindhornae* and *T. collina*. However *T. apicalis* which was the least abundant bee in UMDF and LMDF was the most populous stingless bee of DEF in the dry season.

Wet season

The data for species rank and abundance of stingless bees during April 2004 - March 2005 during the wet season are presented in Appendix B Table 8. A total of 4,395 bees were collected and catches ranged from 40 (*T. canifrons*) and 88 (*T. melina* and *L. cacciae*) to 2,211 specimens (*T. ventralis*). As in the dry season, the dominant species was *T. ventralis*. The second most abundant species was *T. sirindhornae*, followed by *T. collina*. When these data are disaggregated according to forest type, a different pattern emerges. However, except for DEF, this pattern is not the same pattern seen in dry season data.

The average numbers of stingless bees at each plot over the four types of forest are shown in Table 4. The results were showed that DDF has the highest average (9.61 ± 2.91 meliponine bees) followed by UMDF, LMDF and DDF respectively. To consider temporal effects, which might affect stingless bees, these data were grouped according to the sampling seasons. This grouping of data showed a difference between sampling seasons in all forest types. There were high numbers of stingless bees at each plot in the wet season and low numbers in the dry season.

Table 4 Average number and deviation of stingless bees counted at individual Honey-bait trap stations during study period (April 2004 to March 2005).

Type of forest	Dry season	Wet season	Mean
dry dipterocarp forest (DDF)	14.55 ± 3.65	4.66 ± 2.16	9.61 ± 2.91
upper mixed deciduous forest (UMDF)	8.29 ± 5.20	3.04 ± 1.66	6.67 ± 3.43
lower mixed deciduous forest (LMDF)	5.81 ± 1.83	2.33 ± 0.85	4.07 ± 1.34
dry evergreen forest (DEF)	2.03 ± 0.73	1.46 ± 0.27	1.75 ± 0.50

The hierarchical clustering routine was applied to the diversity and abundance data to compile similarity measures among the four types of forest (Figure 29). At the 75 percent similarity level the sites separate into 3 groups. At the 60 percent similarity level DDF clusters with LMDF and UMDF and there are only 2 groups. The resulting dendrogram illustrates that DEF was clearly distinguished from other types of forest (100% dissimilarity) and that stingless bee diversity and abundance were the most similar in UMDF and LMDF (100% similarity).

Similarity by Jaccard

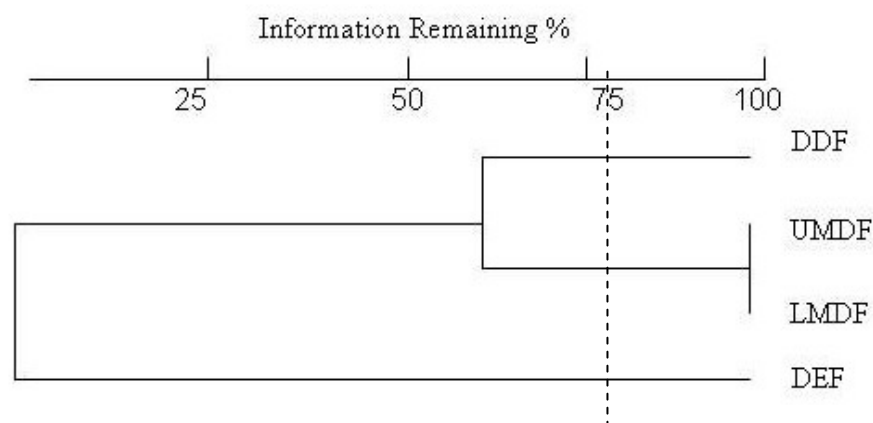


Figure 29 A dendrogram of the similarity of stingless bees in the four types of forest.

A CCA was performed on a primary data matrix consisting of log-transformed numbers of stingless bee individuals from all four types of forest for 11 stingless bee species, and a secondary matrix with two environmental variables (relative humidity and temperature). The analysis made it possible to distinguish groups of stingless bees. In particular, the group comprising *T. collina*, *T. terminata*, *T. ventralis*, *L. cacciae* and *T. sirindhornae* had a positive relationship with temperature; the species of the group increased in abundance with rising temperature and decreased in abundance with increasing relative humidity (R.H.). Another group, comprising *T. sirindhornae* and *P. pendleburyi*, had a positive relationship with relative humidity (R.H.), increasing in abundance with rising relative humidity (R.H.) and decreasing in abundance with rising temperature. *T. melina*, *T. canifrons*, *T. thoracica*, *T. apicalis* and *T. fuscobalteata* had no consistent relationship with the two environmental variables (Figure30).

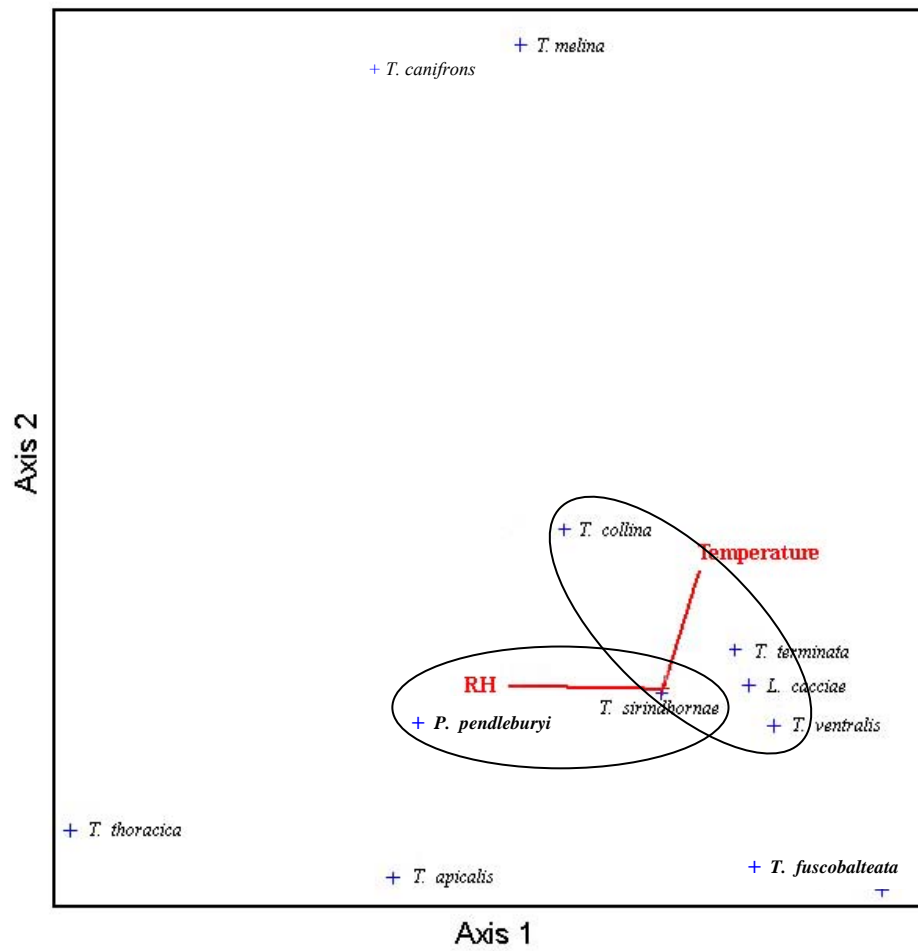


Figure 30 Ordination diagram from the CCA of a primary matrix of the log-transformed totals of stingless bees collected from four types of forest in Thong Pha Phum District, Kanchanaburi Province and a secondary matrix of two environmental variables and their canonical coefficients.

3.2 Seasonal changes of the dominant species

The changes in community structures of stingless bees were studied over the study period. Changes in community structure were examined using similarity. The similarity of the species composition of stingless bee communities between successive months was examined for a one-year period, using the Sorensen Similarity Index and the results are shown in Figure 31. In general, similarity of stingless bee composition increased in the dry season and decreased in the wet season. Similarity decreased in UMDF in the late dry season.

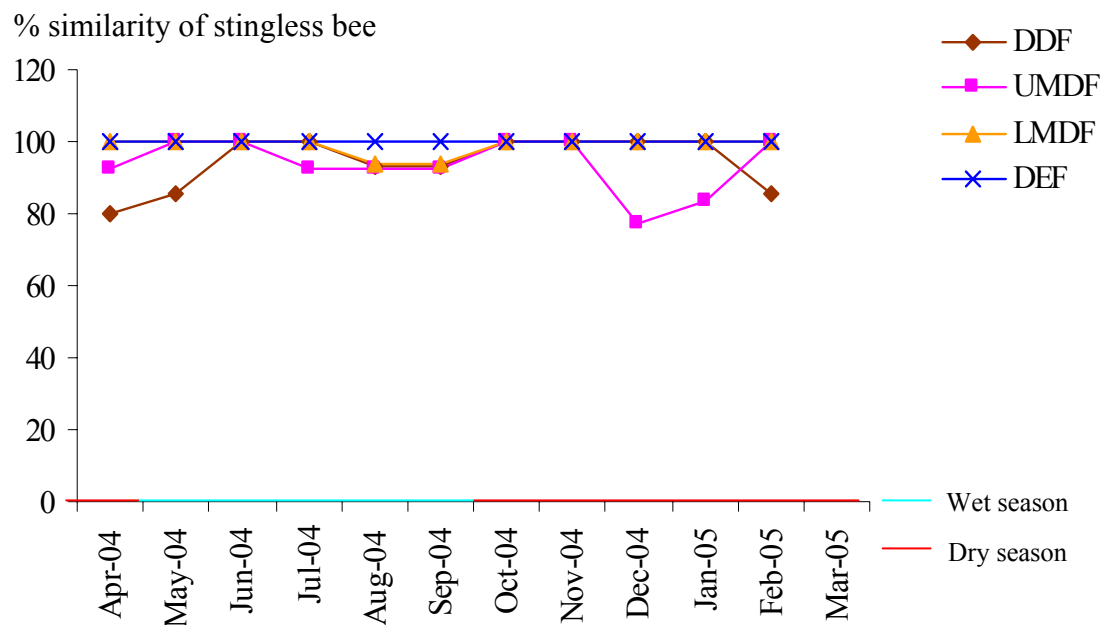


Figure 31 Change in similarity between successive months over study period.

The same species were found in each month in DEF, resulting in the flat line for this forest types in Figure 31. In general, different species were recorded from month to month in UMDF, LMDF and DDF.

Figure 32 shows the seasonal changes in the number of individuals of stingless bees during the study period in four types of forest.

The bee populations of each type of forest were observed to fluctuate inconsistently during the study period. However, some common trends can be seen. The number of individuals showed clear seasonal changes, although catches from day to day depended on weather conditions. In general, the numbers of stingless bees were considerably lower during the wet season and the population trended upwards as the dry season set in. DDF was exceptional in May and July in having a high population, principally as a result of the high populations of *T. ventralis* in these months (Figure 32). The lowest population levels in any type of forest were recorded in the early wet season (May – August) and these increased steadily with the onset of the dry season (September – December), with some fluctuations continuing until March. The highest population (954 bees collected) was recorded in DDF in January 2005. The populations of stingless bees in all four types of forest in the dry season were higher than those in the wet season.

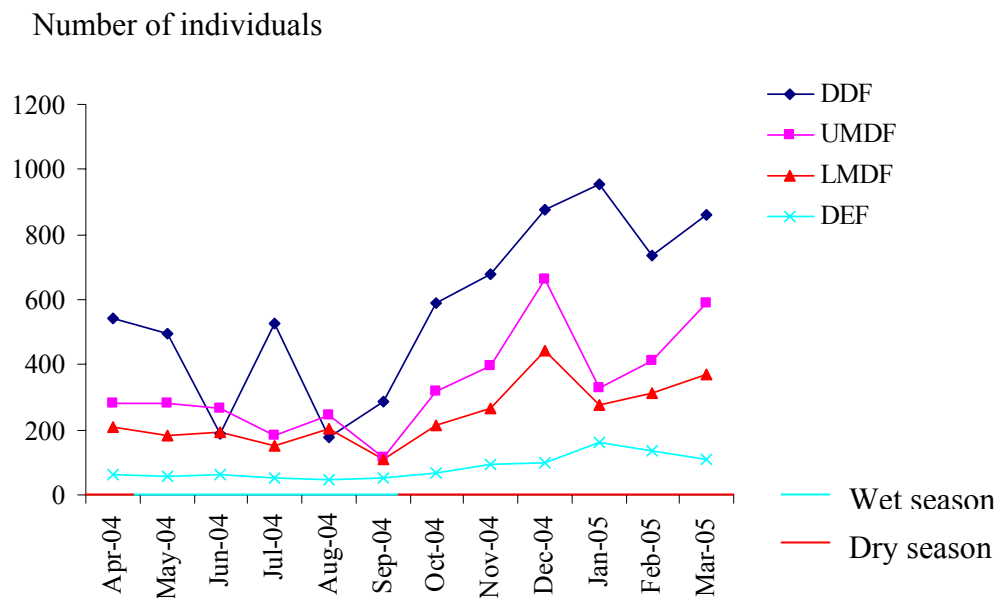


Figure 32 Seasonal changes in the population numbers of stingless bees in the four types of forest from April 2004 to March 2005.

Figure 33 shows seasonal changes in abundance of the dominant species (3 species) over the study period. For the dominant species, abundances were lower in the wet season than in the dry season. In the dry season, population changes were variable among species. The population of dominant species fluctuated inconsistently. In general, the populations of each species in the dry season were higher than those in the wet season. *T. ventralis* in DDF was an interesting exception with a population peak (439 bees captured) in May 2004 during the wet season. In UMDF *T. sirindhornae* was exceptional in that wet season (June) catches indicated higher populations than in some dry season months (November 2004 and January 2005). Nevertheless, the highest population number of *T. sirindhornae* (201 individuals) was recorded in the dry season (March 2004).

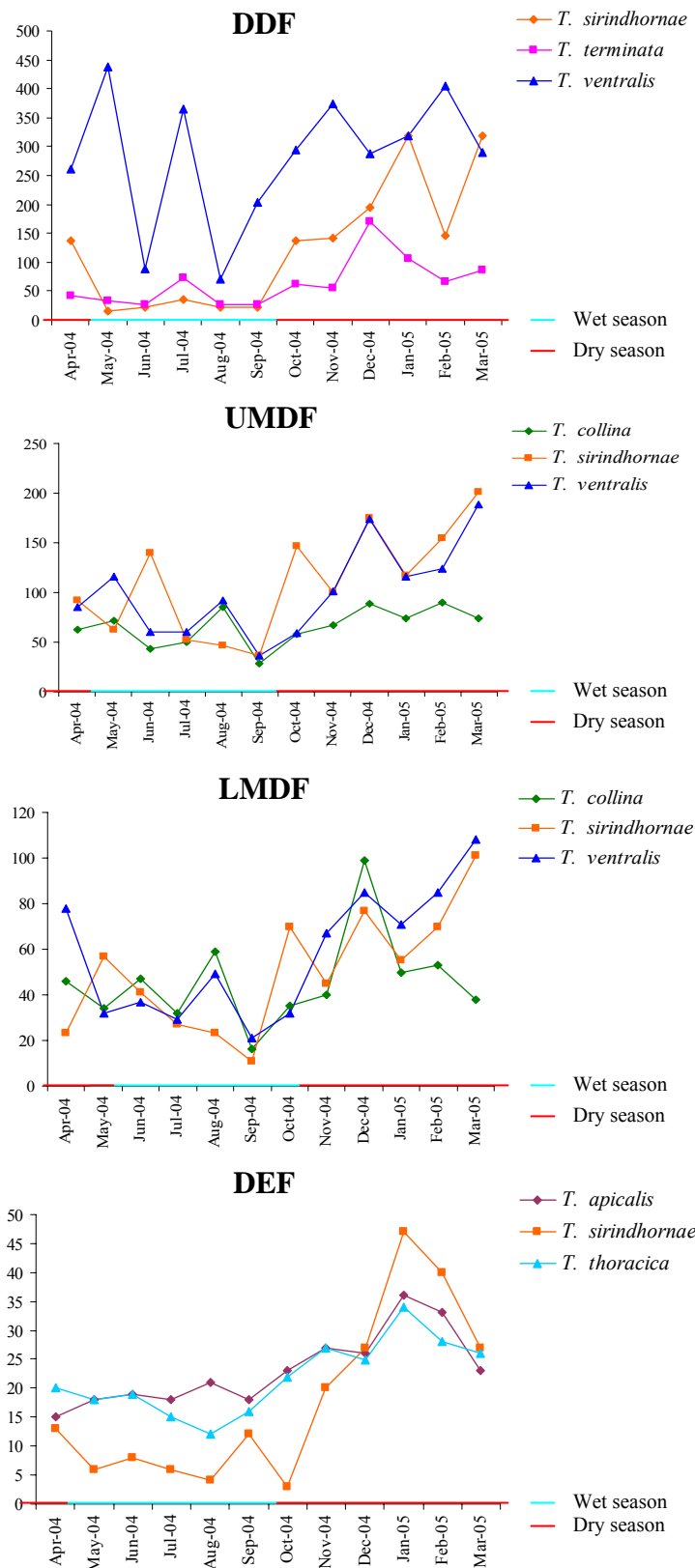


Figure 33 Seasonal trends of the abundance of dominant species in four types of forest during the study period.

3.3 Diversity indices and Evenness of stingless bee species

Variation in the diversity indices (Shannon–Weiner diversity) and Evenness for stingless bees over the four types of forest ecosystem were calculated from the species richness data. Diversity indices were calculated for combined data and separated for wet and dry seasons; these calculations are summarized in Table 5.

The results showed that LMDF has the highest diversity index (0.86) followed by UMDF, DEF and DDF (0.68, 0.67 and 0.63 respectively). DDF and LMDF obtained the highest Evenness figure (0.96), followed by LMDF, UMDF and DEF with Evenness figures of 0.90, 0.80 and 0.67 respectively.

Diversity and evenness indices were mostly greater in dry season sampling compared to wet season sampling.

In DDF, UMDF and DEF, stingless bees exhibited greater diversity indices (H'), 0.69, 0.69 and 0.68 respectively, in the dry season compared to 0.64, 0.62 and 0.41 respectively, in the wet season. However, the diversity index of stingless bees in LMDF was higher in the wet season (0.85) compared to the dry season (0.84).

Similarly DEF, UMDF and DDF stingless bee data showed greater Evenness (0.97, 0.82 and 0.72 respectively) in the dry season compared to 0.91, 0.73 and 0.50 for these forest types in the wet season. However, Evenness in LMDF was higher in the wet season (0.90) compared to the dry season (0.89).

Table 5 Diversity indices and Evenness of stingless bees in the four types of forest during the dry and wet seasons from April 2004 to March 2005.

Type of forest	Diversity indices			Evenness		
	All year	Dry season	Wet season	All year	Dry season	Wet season
dry dipterocarp forest	0.63	0.69	0.41	0.67	0.72	0.50
upper mixed deciduous forest	0.68	0.69	0.62	0.80	0.82	0.73
lower mixed deciduous forest	0.86	0.85	0.84	0.90	0.89	0.90
dry evergreen forest	0.67	0.68	0.64	0.96	0.97	0.91

¹ Shannon-Weiner diversity index (H') values

Presence-absence data were used to compile (similarity) indices of stingless bees in the four types of forest (Figure 34). At the 75 percent similarity level the sites separate into 3 groups. At the 60 percent similarity level DDF clusters with LMDF and UMDF and there are only 2 groups. The resulting dendrogram illustrates that DEF was clearly distinguished from other types of forest (100% dissimilarity) and that stingless bee diversity and abundance were the most similar in UMDF and LMDF (100% similarity).

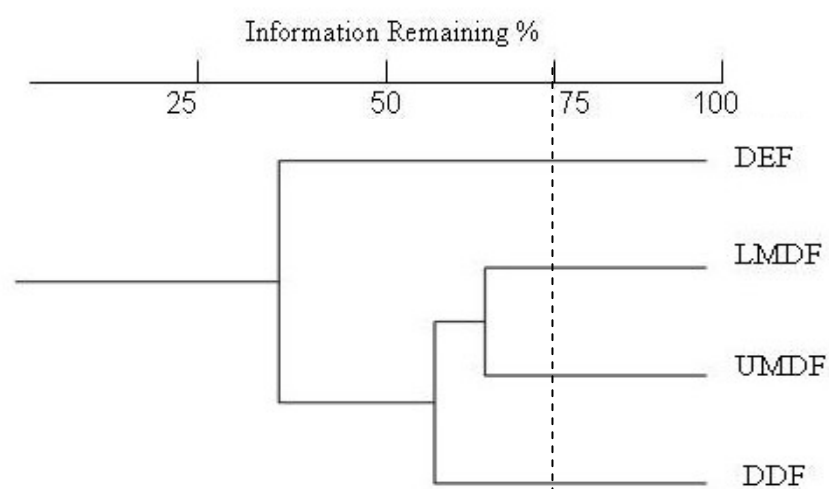


Figure 34 A dendrogram of the diversity indices of stingless bees in the four types of forest.

4. Nests and nest density of stingless bees

4.1 Nests and nest aggregation

A total of 103 natural nests of 15 species of stingless bees were recorded in the four different forest types. Table 6 summarizes the nest types (either “base” or “cavity”) and nest height for the different species. Clearly the different species had distinct preferences in nesting. Cavity nests formed the majority of detected nests (71.84%). The majority of species (13 of 15) were cavity nest and most of these (10 of 15) were exclusively so. Among the species that were exclusively cavity nesting, *T. ventralis*, a medium-sized black bee (~4.5 mm body length), was by far the most common species (accounting for 15.53 % of all nests), followed by *T. terminata* (~5.5 mm; 13.59 %), *T. sirindhornae* (~3 mm; 11.65 %) and *T. apicalis* (~7.5 mm; 7.77 %). The most common species, was the predominantly base-nesting species *T. collina* (~6 mm; 20.39 %). *T. ventralis* produced the largest nests, including one nest that was an impressive 18 m above the forest floor.

Table 6 reveals that the average height of the nests of *Trigona ventralis*, a common, cavity-nesting stingless bee at Thong Pha Phum, was 11.46 m. This suggests that the data for Thong Pha Phum provide a realistic comparison between cavity-and base-nesting stingless bees. Four species were recorded nesting at heights above 5 m: *T. ventralis*, *T. terminata*, *T. sirindhornae* and *T. apicalis*.

Thirteen of the 22 individual nest trees harbored more than one nest. The average number of nests per tree was 3.96 and the average number of species nesting per tree was 2.3. The maximum number of bee nests discovered in a single tree (*Ficus* sp.) was an astonishing 26 nests. This tree hosted no fewer than seven bee species.

At Thong Pha Phum, the most common cavity-nesting species overall were the species most likely to be found co-existing in trees and the most common associations involved the most commonly encountered, cavity-nesting species. Thus, the most

common associations were: *T. collina* x *T. sirindhornae*, *T. collina* x *T. terminata*, and *T. collina* x *T. apicalis*, *T. ventralis* x *T. apicalis*, *T. terminata* x *T. sirindhornae*, and *T. sirindhornae* x *T. apicalis*. These species were the five most commonly encountered species (Table 6). Appendix B Table 9 additionally reveals that three of the most commonly encountered species commonly form conspecific aggregations. In fact, the two most common associations were *T. ventralis* x *T. ventralis* and *T. sirindhornae* x *T. sirindhornae*. *T. sirindhornae* also nested alone.

At Thong Pha Phum Dipterocarpaceae and Moraceae hosted the majority of nest aggregations and the number of nests per tree increased with tree diameter. Only one of the trees hosting nest aggregations was less than 150 cm in diameter at breast height. The largest number of nests was found in a large *Ficus* (family Moraceae). Commonly, *Ficus* begin their life supported by another host tree. Gradually, the *Ficus* envelopes and overgrows the doomed host which slowly rots away. Presumably, the cavities within a *Ficus* left by the former host provide good nesting sites for stingless bees.

Table 6 shows the data tested for differences among the five most abundant species, *T. collina*, *T. ventralis*, *T. terminata*, *T. sirindhornae* and *T. apicalis*. Frequencies of numbers of nests in a 5x3 contingency table (species x type of aggregation) were clearly heterogeneous ($\chi^2 = 24.74$; N=77; df=6; p<0.01). Figure 35 shows that the majority of aggregated nests were found in association with other species, i.e. these were mostly mixed aggregation. The *T. sirindhornae* nests were found in association with conspecifics, although mixed with other species were also common. Colonies of *T. apicalis* frequently nested alone or singly in association with other species.

Table 6 Number of nests, nest type and nest height of nests of stingless bee species.

Species	No.of Nests	No. of base nests	No. of cavity nests	Height of cavity nests (m)		
				Mean	Min	Max
<i>T. collina</i>	26	19	7	1.38	0.8	4.5
<i>T. ventralis</i>	16	0	16	11.46	2.8	18
<i>T. terminata</i>	14	0	14	4.26	0.2	8.9
<i>T. sirindhornae</i>	12	0	12	2.7	1.9	9
<i>T. apicalis</i>	9	1	8	3.54	1.7	6.7
<i>T. pagdini</i>	5	0	5	1.9	0.9	2.5
<i>Trigona</i> sp.1	5	0	5	2.6	0.2	0.7
<i>P. pendleburyi</i>	5	4	1	0.9	0.3	2.2
<i>T. melanoleuca</i>	3	0	3	4.5	0.3	0
<i>T. melina</i>	2	2	0	0	0	0
<i>L. cacciae</i>	2	0	2	3.3	1.7	4.9
<i>T. canifrons</i>	1	0	1	4.9	4.9	4.9
<i>T. atripes</i>	1	1	0	0	0	0
<i>T. thoracica</i>	1	0	1	0.3	0.3	0.3
<i>T. fuscobalteata</i>	1	0	1	2.7	2.7	2.7
Total	103	29	74			

Table 7 Degree of nest clustering and the tendency to form monospecific and/or mixed nest aggregation in individual nest trees of stingless bee species.

Species of stingless bees	No. of nests	No. of nests trees	Monospecific	Mixed	Individual	No. of nests in aggregation	No. of nests in aggregation (%)
<i>T. collina</i>	26	3	2	22	2	24	92.30
<i>T. ventralia</i>	16	5	2	13	1	15	93.75
<i>T. terminata</i>	14	4	0	14	0	14	100
<i>T. sirindhornae</i>	12	5	4	7	1	11	91.67
<i>T. apicalis</i>	9	7	0	5	4	5	55.56
<i>T. pagdeni</i>	5	3	0	5	0	5	100
<i>Trigona</i> sp.1	5	4	1	2	2	3	60
<i>P. pendleburyi</i>	5	3	0	4	1	4	80
<i>T. melanoleuca</i>	3	3	0	2	1	2	66.67
<i>L. cacciae</i>	2	3	0	2	0	2	100
<i>T. canifrons</i>	1	1	0	1	0	1	100
<i>T. fuscobalteata</i>	1	1	0	1	0	1	100

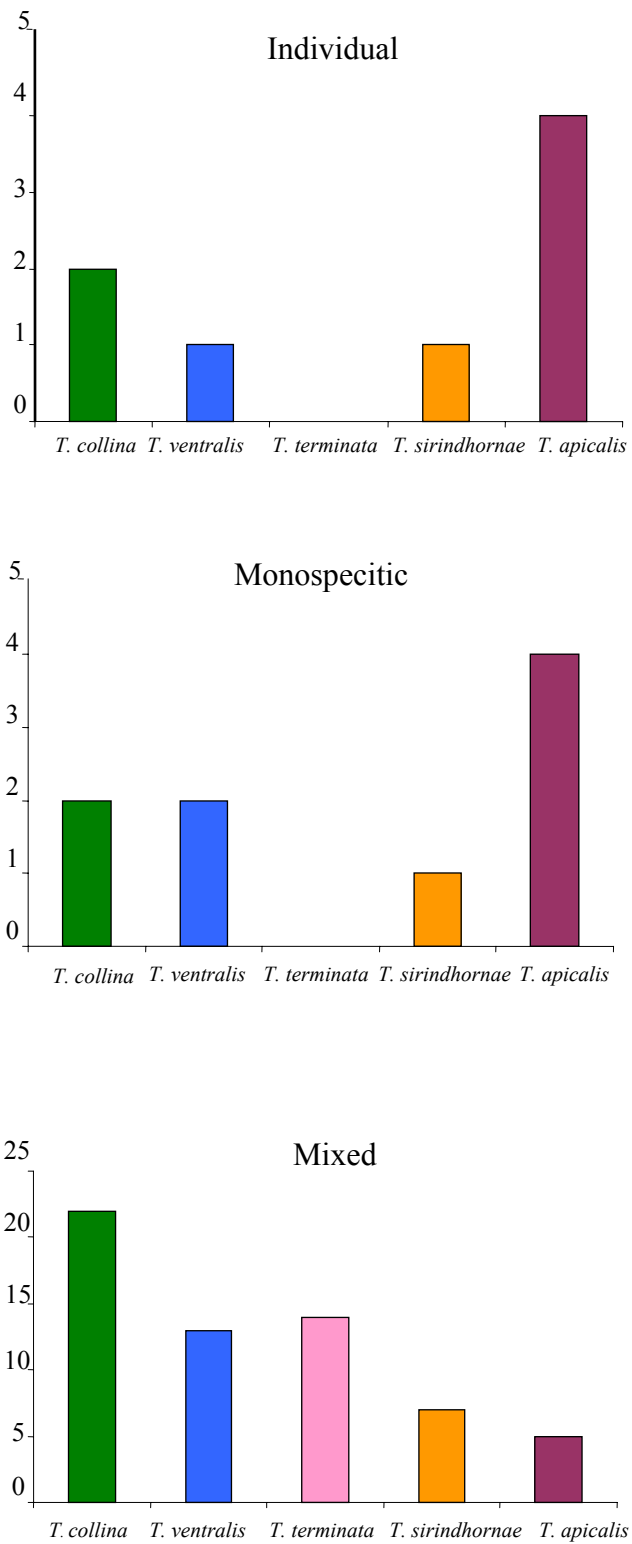


Figure 35 Frequency of nests of dominant species of stingless bees found singly or in aggregation with other colonies.

4.2 Nests and nest density

Table 8 shows the data for nests and nest density in four types of forest between 2004-2006. A total of 103 stingless bee nests of 15 species were located during the quantitative nest survey. Among these 15 species, *T. collina* was by far the most abundant species (28.41 % of all nests), followed by *T. ventralis* (19.06 %) and *T. terminata* (12.58 %). Nest densities vary across the four forest types. Most of the stingless bee species predominantly nest in the cavities of trees. However, the species whose nests were most commonly encountered, *T. collina*, is predominantly a base-nesting species. The next three most commonly encountered species all nest exclusively in tree cavities.

Nest densities were significantly different between the types of forest (DDF, UMDf, LMDF and DEF) over the three years of the study (in 2004: $\chi^2=44.44$; N=103; df=3; p<0.01, in 2005: $\chi^2= 41.49$; N=91; df=3; p<0.01 and in 2006: $\chi^2=32.28$; N=84; df=3; p<0.01) and ranged from 0.66 to 15.66 nests/ha. The 15.66 nest/ha of LMDF were outstanding and represent the highest stingless bee nest densities. The lowest nest densities were found in DEF (0.66 nests/ha).

The Table 8 summarizes nest density data for consecutive years of the study period. The results show progressive and distinct reductions in the numbers of nests. Nest density was highest in 2004 (on average 8.58 nests/ha) and decreased in 2005 and 2006 (7.58 and 7.0 nests/ha respectively) ($\chi^2=9.21$; N=278; df=2; p<0.01).

Nest density generally declined over the three years of the study. This was a result of progressive and distinct reductions in the numbers of nests of the most commonly encountered species, *T. collina*, and slight reductions in the frequency of nests of several, less common species, such as *T. terminata*, *T. sirindhornae*, *T. pagdini*, *P. pendleburyi*, *T. melanoleuca* and *T. melina*. The decline in nest density was not uniform, however. Densities of the second most common species,

T. ventralis, increased slightly from year to year, in three different forest types. For other, scarce species, nest density did not appear to vary from year to year, irrespective of whether nest counts were disaggregated according to forest type or were combined.

For the three species whose nests were most commonly encountered during the study, *T. collina*, *T. ventralis* and *T. terminata*, nest density varied dramatically between forest types.

T. collina nested commonly in UMDF and LMDF (densities ranging from $6/3 - 18/3 = 2.00-6.00$ nests/ha), less frequently in DEF (density $2/3 = 0.66$ nests/ha), and was absent from DEF.

T. ventralis nests were at more or less comparable densities in DDF and UMDF ($3/3-8/3 = 1.00-2.66$ nests/ha; $8/3-9/3 = 2.66-3.00$ nests/ha respectively), were slightly scarcer in LMDF ($3/3-4/3 = 1.00-1.33$ nests/ha), and were not detected at all in DEF.

The pattern of nest densities for *T. terminata* was more similar to that of *T. collina* than to that of *T. ventralis*. *T. terminata* nests were found in UMDF and LMDF ($5/3-8/3 = 1.66-2.66$ nests/ha and $5/3-6/3 = 1.66-2.00$ nests/ha respectively), but were not seen in either DDF (*T. collina* was absent from DDF) or DEF (where *T. collina* nests were infrequent).

Because the numbers of nests of species other than *T. collina*, *T. ventralis* and *T. terminata*, are rather small, it is difficult to make further generalisations with the great confidence. However, the data do suggest the following:

1) Nests were most commonly encountered in LMDF and UMDF. Twelve of the 15 species nested in LMDF, at densities between 12.0 and 15.66 nests/ha. Nine of the 15 species nested in UMDF, at densities between 9.33 and 10.33 nests/ha.

Nests were less commonly encountered in DDF. Six of the 15 species nested in this forest type, at densities between 4.33 and 6.66 nests/ha.

Only *T. collina* and *T. apicalis* nested in DEF and only at low densities (0.66 nests/ha for both species).

2) Most species (9 of 15) nested in more than one forest type. The uncommonly encountered nests of *T. melanoleuca*, *T. melina*, *T. canifrons*, *T. atrpes* and *T. thoracica* were found only in LMDF.

3) In DDF, UMDF and DEF, in each year, five species account for 85% to 100% of the nests. In LMDF, the top five species account for a smaller percentage of the nests (between about 67% and 76% of the nests).

4) Species tended to be consistently present or absent from a forest type from one year to the next. For example, the commonly encountered *T. collina* was consistently absent from DDF and consistently present in UMDF, LMDF and DEF. Similarly, the infrequently encountered *T. melanoleuca* was consistently absent from DDF, UMDF and DEF, and consistently present in LMDF. Nests of six relatively infrequently encountered species known to nest in a particular forest type, were not detected in that forest type in one or two years of the study period.

5) There seems to be little correlation between nest and forest types. *T. collina* and *P. pendleburyi* are both predominantly tree-base nesters. However, *T. collina* was most common in LMDF while *P. pendleburyi* was absent from LMDF. *T. collina* was absent from DDF; *P. pendleburyi* nests were most numerous in DDF. It is unlikely that *P. pendleburyi* displaces *T. collina* from tree base nesting sites in DDF. Nesting sites do not appear to be limiting and *P. pendleburyi* remains a scarce species anyway. Similarly, *T. ventralis* and *T. terminata* are both exclusively cavity nesters. However, *T. ventralis* was present in all forest types except DEF while *T. terminata* was present only in UMDF and LMDF types.

Table 8 Counts and densities of nests and nest trees of stingless bees found during quantitative nest surveys of four forest sites during 2004-2006.

Type of forest (Site)	DDF			UMDF			LMDF			DEF			Total				
Year	04	05	06	04	05	06	04	05	06	04	05	06	04	05	06	Mean	%
Area searched (ha)	3	3	3	3	3	3	3	3	3	3	3	3	12	12	12		
No. nests	20	16	18	33	31	28	48	43	36	2	2	2	103	92	84		
<i>T. collina</i>	0	0	0	6	8	10	20	18	13	0	0	0	28	26	25	26.33	28.41
<i>T. ventralis</i>	5	5	8	8	8	9	3	3	4	0	0	0	16	16	21	17.66	19.06
<i>T. terminata</i>	0	0	0	8	7	5	6	5	4	0	0	0	14	12	9	11.66	12.58
<i>T. sirindhornae</i>	4	3	3	3	3	2	5	4	3	0	0	0	12	10	8	10	10.75
<i>T. apicalis</i>	3	2	2	1	1	1	3	3	3	2	2	2	9	8	8	8.33	8.99
<i>T. pagdini</i>	0	0	0	3	2	1	2	2	2	0	0	0	5	4	3	4	4.32
<i>Trigona</i> sp.	3	3	3	2	1	0	0	0	0	0	0	0	5	4	3	4	4.32
<i>P. pendleburyi</i>	4	3	2	1	1	0	0	0	0	0	0	0	5	4	2	3.67	3.96
<i>T. melanoleuca</i>	0	0	0	0	0	0	3	3	3	0	0	0	3	3	3	3	3.24
<i>T. melina</i>	0	0	0	0	0	0	2	1	0	0	0	0	2	1	0	1	1.08
<i>L. cacciae</i>	1	0	0	0	0	0	1	1	0	0	0	0	2	1	0	1	1.08
<i>T. canifrons</i>	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1.08
<i>T. atripes</i>	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1.08
<i>T. thoracica</i>	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0.67	0.72
<i>T. fuscobalteata</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0.67	0.72
Nests / ha	6.66	5.33	4.33	11	10.33	9.33	16	14.33	12.00	0.66	0.66	0.66	8.58	7.66	7		

4.3 Stingless bee nest entrances

Usually the nest entrance is composed of gum and propolis (collected by the bees). In some species sand is mixed with the construction material.

***Lisotrigona cacciae* (Nurse)** (Figure 36a)

Exposed tube short (2–3 cm); mostly horizontal; external surfaces rough, with tiny, irregular protrusions, dark grey to blue near base, becoming pale yellow apically. Tube expanded only very slightly at apex; free margins rough, in side view at right angles to axis of tube; without conspicuous landing platform; in axial view the opening is round to slightly oval; mouth of entrance 1.0–2.0 cm; usually light brown. Mouth of the entrance 1.0 by 2.0 cm and tube length 2-3 cm.

***Pariotrigona pendleburyi* Schwarz** (Figure 36b)

Nest opening more or less flush with surface of substrate, rounded and narrowing to concealed tube, surrounding substrate covered by resinous material. Entrance with neither exposed tube, free-standing, expanded entrance nor defined landing platform. Mouth of entrance 1.7 by 2.0 cm.

***Trigona terminata* Smith** (Figure 36c)

Exposed tube generally long (7–50cm), slightly downwardly directed, progressively widening towards apex, thin walled; external surface smooth; basally reddish brown, apically dirty white. Tube expanding apically to form delicate, resinous trumpet; free margins ragged, lower margin protruding beyond upper margin to form distinct landing platform, so that in side view free margins are slightly oblique to axis of tube; in axial view opening oval to slightly pear-shaped; mouth of the entrance 2.5 - 3.0 by 2.8 - 3.5 cm. Tube very soft and sticky. Substrate adjacent to

entrance coated with white material; this sometimes red or brown, probably depending on the species of tree from which the gum originates.

***Trigona ventralis* smith** (Figure 36d)

Exposed tube generally long (5–35 cm), thin walled, parallel sided for most of its length, angled downwards from base; external surface smooth; basally slightly and narrowly greyish, mostly ivory white. Tube slightly expanded into very weak trumpet; free margins smooth, lower margin protruding slightly beyond upper margin to form landing platform, so that in side view free margins slightly oblique to axis of tube; in axial view opening slightly oval; mouth of entrance 2.0-2.5 cm by 2.2–2.8 cm. In general the nest entrance is very similar to that of *T. terminata*, although smaller. Tube very soft and sticky; sometimes red or brown, probably depending on the species of tree from which the gum originates.

***Trigona canifrons* Smith** (Figure 37e)

Entrance with neither exposed tube nor expanded trumpet. In shape entrance ear-like; mouth entrance 5 cm by 8-10 cm. Entrance very hard, formed by a mixture of sand and gum. This species is very aggressive and there are usually many stingless bees assembled to protect the nest entrance.

***Trigona thoracica* Smith** (Figure 36f)

Entrance comprises low, rounded mound with apical opening in the form of a short, broad, inverted cone inside the mound; external tube and trumpet absent. Mound basally with rough exterior surface, this sometimes with irregular flanges, apically with weak, more-or-less concentric ridges surrounding opening, ridges continuing slightly onto interior surface of opening. Opening circular in axial view, without sharply defined free margins; mouth of entrance 12–13 cm by 13–15 cm. Mound pinkish; interior surfaces of opening with irregular silver-grey markings. Nest entrance very hard and mixed with sand and gum, almost reddish.

***Trigona apicalis* Smith** (Figure 36g)

Exposed tube generally short (15–25 cm), horizontal, expanding rapidly from base to short, wide, asymmetrical trumpet; walls very strong, resinous with gum and sand. External surfaces rough, blackened. Free margins of trumpet vertical, so that margins are at right angles to the axis of the entrance and there is no well-defined landing platform. Opening in axial view round when construction begins; mouth of entrance 2.3–3.0 cm by 8–10 cm. Entrance very hard and mixed with sand and gum; sometimes red or brown, probably depending on the tree from which the gum originates.

***Trigona melanoleuca* Cockerell** (Figure 36h)

Exposed tube elongate (35–60 cm), parallel sided, basally irregular, otherwise slightly taller than wide in cross-section; curving irregularly downwards; External surface smooth; predominantly yellowish brown, darker brown basally and dirty white apically. Apex scarcely expanded, free margins obliquely truncated so that lower margin strongly protruding to form distinct landing platform. Substrate adjacent to entrance coated with white material. Entrance very hard; mouth of entrance 2-3 cm by 5-6 cm.

***Trigona atripes* Smith** (Figure 36i)

Exposed tube elongate (25 cm), parallel sided, rounded in cross-section; more or less straight and directed upwards; external surfaces rough; predominantly dark colored, apically narrowly cream-colored. Opening only very slightly expanded compared to tube; free margins at right angle to axis of tube; without defined landing platform; mouth of entrance 1.2 cm by 1.5 cm. Entrance very hard and similar to that of *T. collina*. Mouth of entrance 1.2 cm by 1.5 cm and tube length 25 cm

***Trigona collina* Smith** (Figure 36j)

Exposed tube generally elongate (2–37 cm), narrowing slightly from base to apex, directed upwards; external surface smooth; basally brown, becoming pale brown over midlength, apically dirty white. Free margins of opening at right angle to axis of tube; smooth; opening round, without landing platform; mouth of entrance 0.8–1.5 cm by 1–1.5 cm.

***Trigona pagdeni* Schwarz** (Figure 36k)

Exposed tube very short (1–3 cm) expanding quickly into a vertically elongate, ear-like entrance funnel; external surfaces rough; dark colored, free margins of opening very dark. Free margins of opening slightly ragged, at right angle to axis of entrance tube; mouth of entrance 2.5–3.0 cm. Entrance very hard, formed by mixture of sand and gum. Mouth of entrance 2.5–3.0 cm. by 2.8–3.5 cm and tube length 1–3 cm.

***Trigona fuscobalteata* Cameron** (Figure 36l)

Exposed tube (2–3 cm) forms a gallery on the substrate that gives rise to multiple exit tubes. Each exit tube narrowing towards the apex, rounded in cross-section, curved or straight; external surfaces rough; white. Openings round in axial view; mouth of entrance 0.6 cm by 2–3 cm.

***Trigona melina* Gribodo** (Figure 36m)

Exposed tube short, more or less horizontal, irregular in cross-section, taller than wide. External surface rough, irregular, in part adapting to substrate, leaves or twigs sometimes incorporated into walls; color grey to black. Apex expanded irregularly, free margins strongly oblique to axis of tube, so that opening is more or less upwards; opening almost rectangular, upper margin short, thickened and vertical; lower margin short, expanded into distinct landing platform; lateral margins, long,

parallel; all margins simple. Entrance very hard, formed by mixture of sand and gum. Mouth of entrance 2.5-3.0 cm by 2.8-3.5 cm.

***T. sirindhornae* Michener & Boongird** (Figure 36n)

External tube moderately long (2–3cm), curved, adhering to substrate; tubes forming irregular ring, with upper part slightly extended and lower part strongly extended, so that whole has appearance of a hollow spindle; resinous, hard. Opening concealed, directed downwards; substrate forming a landing surface; mouth of entrance 1- 2 cm by 2-3 cm.

***Trigona* sp. 1** (Figure 36O)

External tube moderately long (3–5 cm), curved, adhering to substrate; tubes forming irregular ring, with upper part slightly extended and lower part strongly extended, so that whole has appearance of a hollow spindle; resinous, hard; external surface polished black. Opening concealed, directed downwards; substrate forming a landing surface; mouth of entrance 2.5 - 3.0 cm by 2.8-3.5 cm.

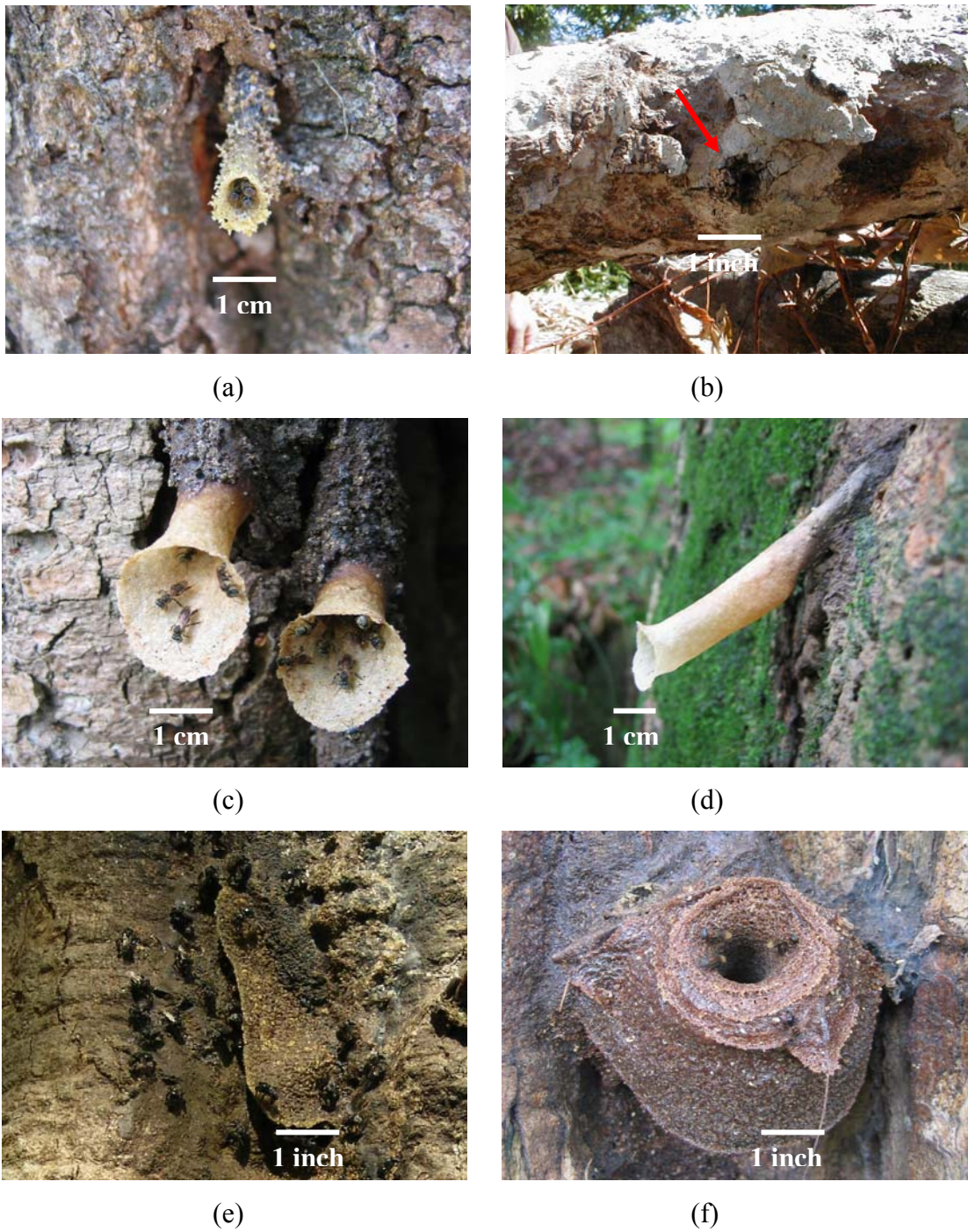


Figure 36 The nest entrances of stingless bees

- a) *L. cacciae* (Nurse)
- c) *T. terminata* Smith
- e) *T. canifrons* Smith

- b) *P. pendleburyi* Schwarz
- d) *T. ventralis* Smith
- f) *T. thoracica* Smith



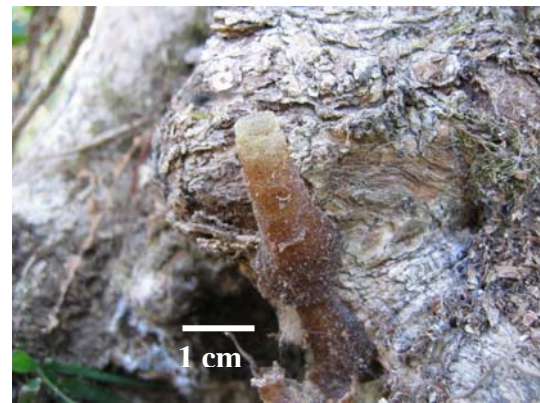
(g)



(h)



(i)



(j)



(k)



(l)

Figure 36 (Continued) The nest entrances of stingless bees

g) *T. apicalis* Smith

i) *T. atripes* Smith

k) *T. pagdeni* Schwarz

h) *T. melanoleuca* Cockerell

j) *T. collina* Smith

l) *T. fuscobalteata* Cameron



(m)



(n)



(o)

Figure 36 (Continued) The nest entrance of stingless bees

m) *T. melina* Gribodo

n) *T. sirindhornae* Michener & Boongird

o) *Trigona* sp. 1

5. Diversity of host plants

5.1 Daily foraging behavior of stingless bees from four types of forest

5.1.1 Foraging behavior of stingless bees from dry dipterocarp forest (DDF) during wet and dry seasons

Figure 37 shows the daily changes in the number of foragers of stingless bees in the wet and dry season in DDF. The highest number of foragers of stingless bees during the wet season was recorded at 10 a.m. followed by 11 a.m. and 2 p.m. and the highest number of foragers of stingless bees during the dry season was recorded at 11 a.m. followed by 12 a.m. and 10 a.m. The numbers of foragers in the morning tended to be higher than the numbers in the afternoon but generally the number of foragers remained steady throughout the day in the dry season.

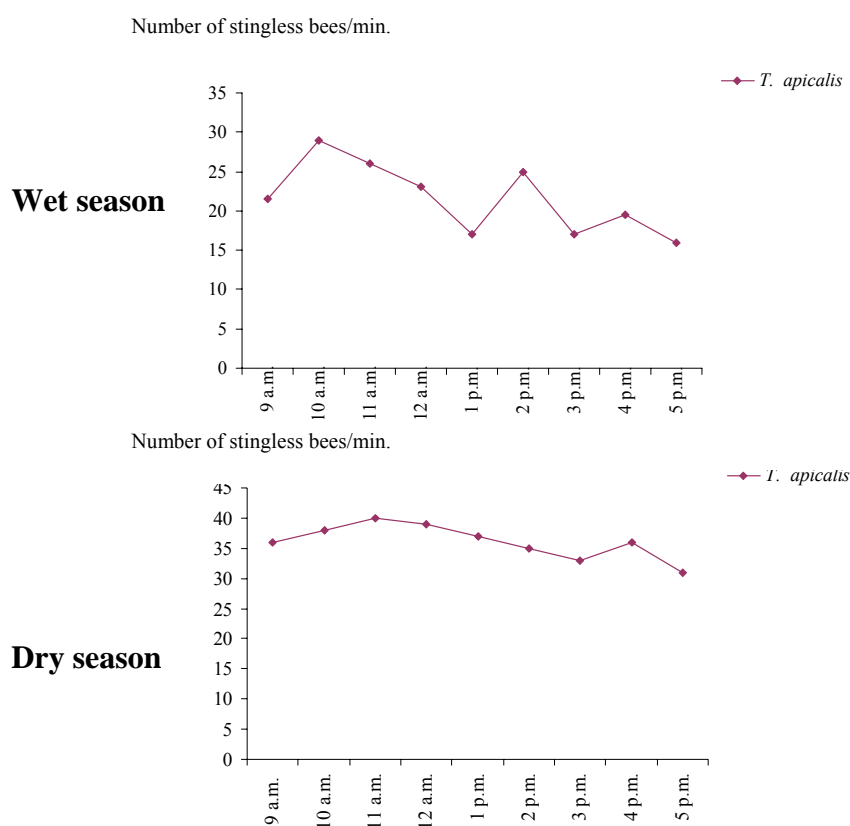


Figure 37 The daily changes (wet and dry seasons) in the number of foragers of *T. apicalis* stingless bees in dry dipterocarp forest (DDF).

5.1.2 Foraging behavior of stingless bees from upper mixed deciduous forest (UMDF) during wet and dry seasons

Figure 38 shows the daily changes in the numbers of foragers of four species of stingless bees in the wet and dry seasons in UMDF. Foraging by each species of stingless bee was observed to fluctuate somewhat inconsistently during the day in the wet and dry seasons. However, some common trends can be seen. In general, the numbers of foragers were greatest between 11 a.m. and 1.00 p.m. and declined as the afternoon progressed. The large species, *T. apicalis* had the largest number of foragers at 9.00 a.m. in both seasons and unusually high forager numbers at 4 p.m. in the wet season. Fluctuations continued until 5 p.m.

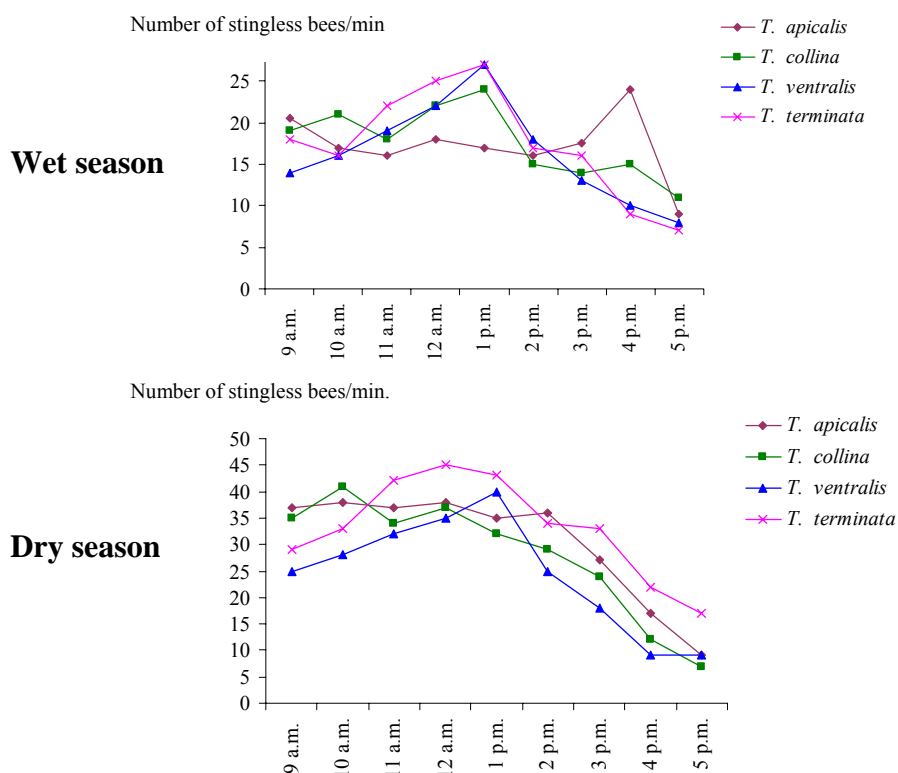


Figure 38 The daily changes (wet and dry seasons) in the number of foragers of four species of stingless bees in upper mixed deciduous forest (UMDF).

5.1.3 Foraging behavior of stingless bees from lower mixed deciduous forest (LMDF) during wet and dry season.

Figure 39 shows the daily changes in the number of foragers for six species of stingless bees in the wet and dry seasons in LMDF. The number of foragers of each species was observed to fluctuate somewhat inconsistently during the day in both seasons. However, some common trends can be seen. In general, numbers of foragers were greater during the morning and declined as the afternoon progressed. The highest numbers of foragers for any species were recorded between 11 a.m. and 1 p.m.. The medium-sized species, *T. collina* was exceptional in having high forager numbers at 10 a.m. in the wet season and 11 a.m. in the dry season. Fluctuations continued until 5 p.m.

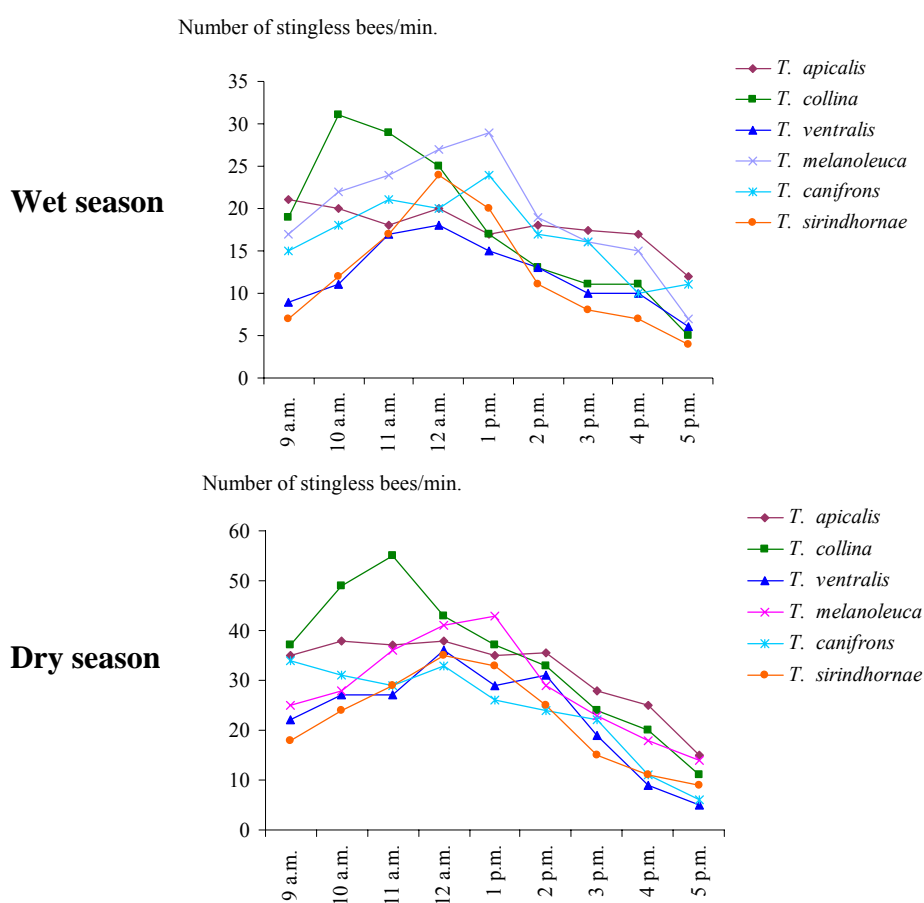


Figure 39 The daily changes (wet season dry seasons) in the number of foragers six species of stingless bee in lower mixed deciduous forest (LMDF).

5.1.4 Foraging behavior of stingless bees in dry evergreen forest (DEF) during wet and dry seasons

Figure 40 shows the daily changes in the numbers of foragers from two colonies of *T. apicalis* in the wet and dry seasons in DDF. The highest number of foragers during the sampling period was recorded at 11 a.m. followed by 10 a.m. and 9 a.m. in wet season and 12 a.m., followed by 1 p.m. and 10 a.m. in the dry season. The number of foragers in the morning tended to be higher than the number in the afternoon. The number of foragers declined steadily until about 5.00 pm.

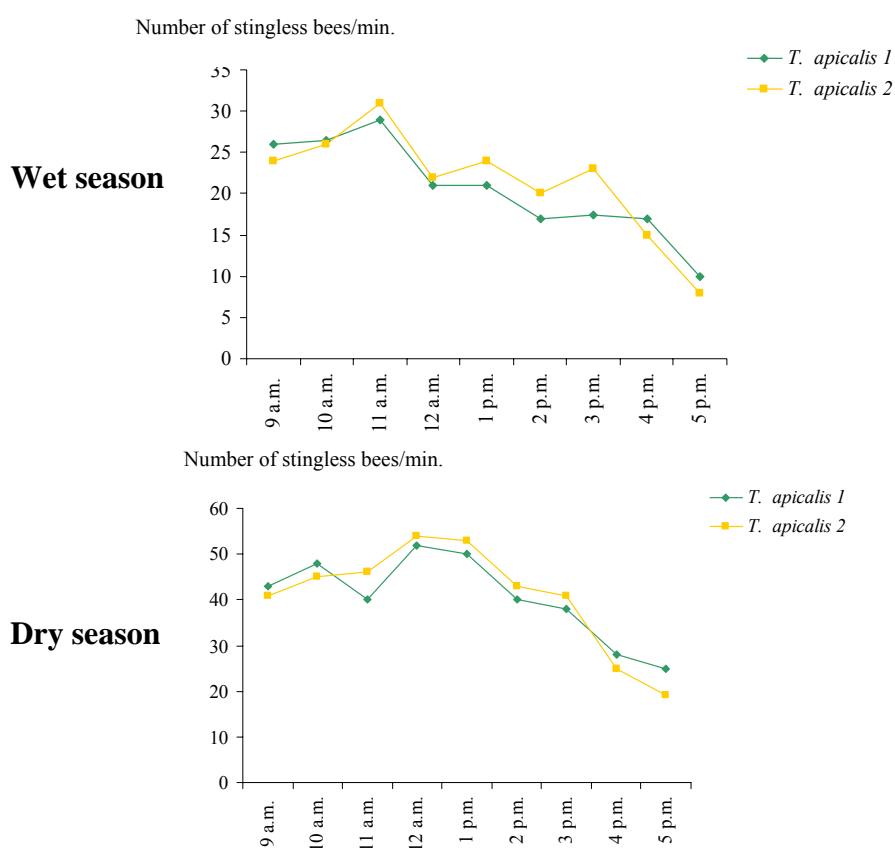


Figure 40 The daily changes (wet and dry seasons) in the number of foragers from two nests of *T. apicalis* in dry evergreen forest (DEF).

5.2 Pollen-foraging behavior

5.2.1 Seasonal pollen-foraging behavior of *Trigona apicalis* from four types of forest

Figure 41 shows the seasonal changes in the percentage of *T. apicalis* that successfully foraged for pollen during the study period in the four types of forest.

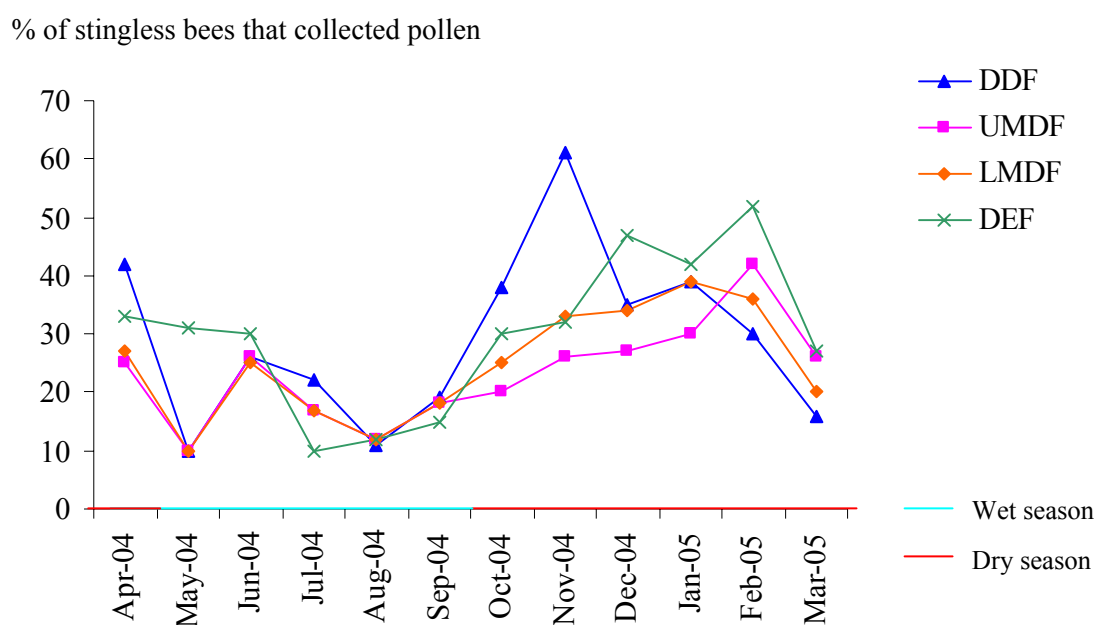


Figure 41 The seasonal changes in the percentage of pollen foraging of *T. apicalis* during the study period in four types of forest.

Pollen foraging in each type of forest fluctuated inconsistently during the study period. However, some common trends can be seen. In general, the percentages of *T. apicalis* successfully foraging for pollen were considerably lower during the wet season and higher in the dry season. The lowest percentages of successful pollen foragers in any type of forest were recorded in the wet season (May – August 2004). In May 2004 commonly only 10% of foragers returned to the nest with pollen. In general, percentages declined as the wet season progressed and increased steadily with the onset of the dry season (September – December 2004), with some

fluctuations continuing until March 2005. Nests in UMDF tended to have lower percentages of pollen foragers. They had the highest or equal highest percentages during only one month and the lowest or equal lowest in no fewer than six months. On the other hand, nests in DEF tended to have higher percentages of pollen foragers. They had the highest or equal highest percentage in seven months and the lowest or equal lowest percentage in only two months.

The highest percentage of successful pollen foraging by *T. apicalis* (61 %) was recorded in DDF in November. The percentages of pollen foraging by *T. apicalis* in all four types of forest in the dry season were higher than those in the wet season. Although the percentage of pollen foraging by *T. apicalis* showed clear seasonal changes, catches from day to day depended on weather conditions.

5.2.2 Daily pollen-foraging behavior during wet and dry season: all forest types

Figure 42 shows the daily changes in the percentage of successful pollen foragers in the wet and dry season during the study period in the four types of forest. Pollen foraging in of each type of forest was observed to fluctuate somewhat inconsistently during the day. However, some common trends can be seen. In general, successful pollen foragers formed a greater percentage of returning stingless bees during the morning and the percentage declined as the afternoon set in. The highest percentages in any type of forest were recorded in the morning (9 a.m. - 11 a.m.) in wet season and later (12 a.m. - 1 p.m.) in the dry season. Fluctuations continued until 5 p.m. In DDF, there was a slight tendency for pollen foraging to remain higher later in the day, than was the case in other forest types in both wet and dry seasons. In UMDF had an unusual peak at 4 p.m. in the wet season.

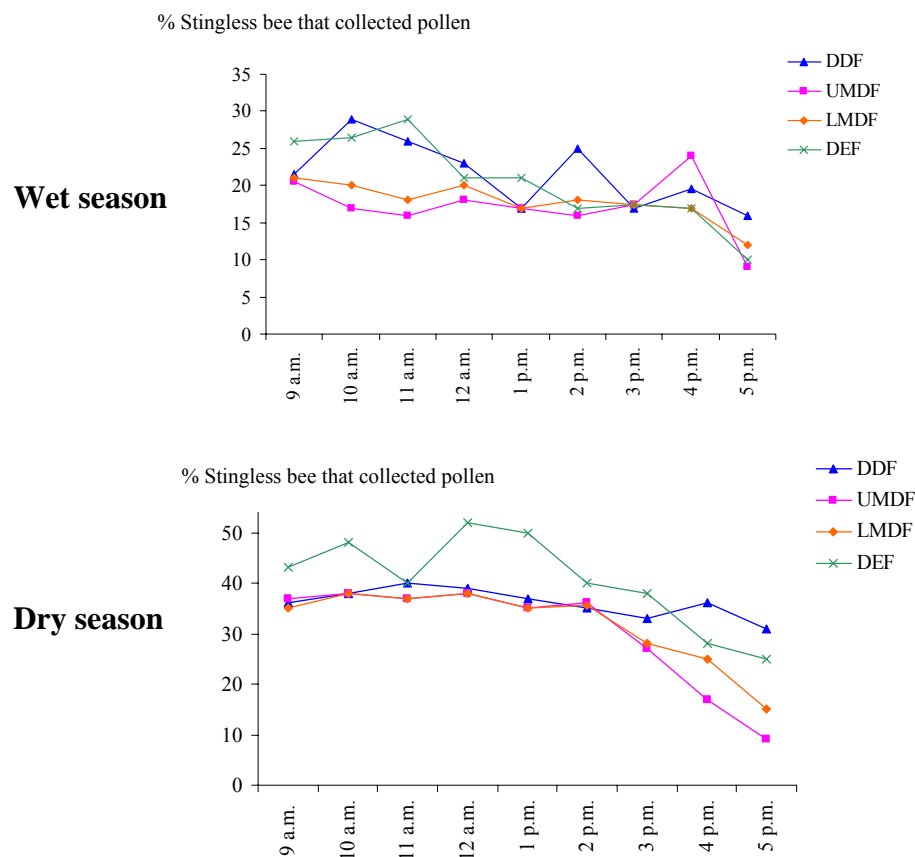


Figure 42 The daily changes (wet season) in the percentage of pollen foraging stingless bees during the study period in four types of forest.

5.3 Pollen-foraging of all stingless bees from four types of forest

5.3.1 Pollen-foraging behavior of stingless bees in dry dipterocarp forest (DDF)

Trigona apicalis was used as a representative of stingless bees in dry dipterocarp forest. The highest percentage of successful pollen foragers in DDF during the sampling period was in November 2004 followed by April 2004 and January 2005, with respectively 61%, 42% and 39% of bees returning to the nest carrying pollen. The percentages of pollen-foraging stingless bees for each month in the dry season were higher than those in the wet season (Figure 43).

5.3.2 Pollen-foraging behavior of stingless bees in upper mixed deciduous forest (UMDF)

Figure 43 shows the seasonal changes in the percentage of pollen foraging by four species of stingless bee in UMDF. Pollen foraging in each species of stingless bee fluctuated inconsistently during the study period. However, some common trends can be seen and the percentage of pollen foragers showed clear seasonal changes. In general, the percentage of pollen foragers was lower in the wet season and higher during the dry season. The lowest percentages of successful pollen foragers in any type of forest were recorded in the wet season (May-August 2004). In May and August 2004 commonly only 7 or 8 % of foragers returned to the nest with pollen. In general, percentages declined as the wet season progressed and increased steadily with the onset of dry season (September-December 2004), with some fluctuations continuing until March 2005. The highest percentage of successful foragers (56%) was recorded for the medium-sized *T. terminata* in February. The same species recorded the least successful batch of foragers (May and August 2004, about 10%). The large-sized species, *T. apicalis* had the highest or equal highest percentages of pollen foragers during the most months (6). The small species, *T. ventralis* had the lowest or equal lowest percentage of pollen foragers during the most months (5).

5.3.3 Pollen-foraging behavior of stingless bees in lower mixed deciduous forest (LMDF)

Figure 43 shows the seasonal changes in the percentage of six species of stingless bees that successfully foraged for pollen during the study period in LMDF. Pollen foraging in each species of stingless bee fluctuated inconsistently during the study period. However, some common trends can be seen. In general, the percentages of stingless bees successfully foraging for pollen were considerably lower during the wet season and trended upwards as the dry season set in. The lowest percentages of successful pollen foragers in any type of forest were recorded in the wet season (May – August 2004). Between May and August 2004 commonly less than 10% of foragers returned to the nest with pollen. In general, percentages declined as the wet season progressed and increased steadily with the onset of the dry season (September – December 2004), with some fluctuations continuing until March 2005. The highest percentage of successful pollen foraging by stingless bees (46 %) was recorded for *T. collina* in February 2005. The percentages of pollen foraging in the dry season were higher than those in the wet season. The percentage of pollen foraging of stingless bees catches from day to day depended on weather conditions.

LMDF had the highest percentage of pollen foragers in only one of the sampling months, but had the lowest percentage in a remarkable nine months.

The large species, *T. apicalis* had the highest percentage of pollen foragers during eight months and the lowest during only one month. The large *T. melanoleuca* and *T. canifrons* each had the highest percentage of pollen foragers in only one month, and like *T. apicalis* had the lowest percentage of pollen foragers in only one month. The small *T. ventralis* and *T. sirindhornae* never had the highest percentage of pollen foragers and *T. ventralis* had the lowest percentage of pollen foragers for nine of the sampling months. No other species was the “worst performer” in more than one month.

5.3.4 Pollen-foraging behavior of stingless bees in dry evergreen forest (DEF)

Trigona apicalis was used as a representative of the stingless bees of Dry evergreen forest. The highest percentage of successful pollen foragers in DEF during the sampling period was in February 2005 followed by December 2004 and January 2005, with respectively 52%, 47% and 42% of bees returning to the nest carrying pollen. Nests in DEF had the highest or equal highest percentage of successful pollen foragers in five of the sampling months and the lowest or equal lowest percentage in four of the sampling months. The percentages of pollen-foraging stingless bees for each month in the dry season were higher than those in the wet season (Figure 43).

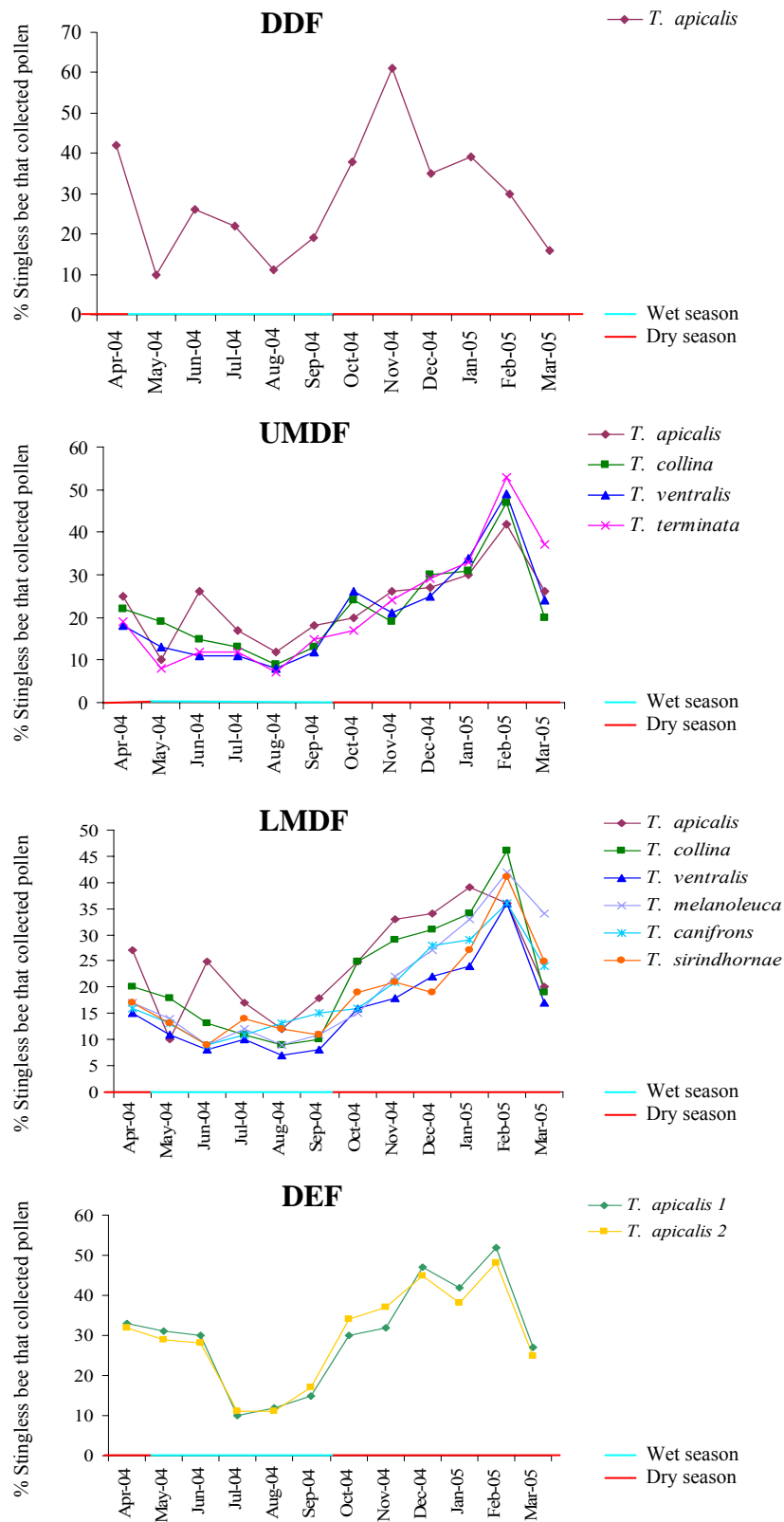


Figure 43 The seasonal changes in the percentage of pollen foraging by stingless bees during the study period in four types of forest.

6. Number of types of host plants from which stingless bees collected pollen in four types of forest

6.1 Foraging behavior of stingless bees in four types of forest during April 2004-March 2005

To examine the effect of the type of forest and season on the number of types of pollen collected by stingless bees, samples were grouped according to the type of forest. This new grouping of data showed that there were only slight differences between the types of forest-as shown in Figure 44.

DDF: The data for DDF comprise the seasonal changes in the number of pollen types collected by *T. apicalis*. The highest number of pollen types collected by *T. apicalis* was recorded in December 2004 and January 2005 (9 types of pollen) (dry season). The numbers of types of pollen collected by *T. apicalis* during each month in the dry season tended to be higher than the numbers in wet season.

UMDF: The pollen types collected by each species of stingless bee in UMDF fluctuated somewhat inconsistently during the study period. In general, the numbers of pollen types were greater in the dry season and declined as the wet season progressed. The highest numbers of pollen types for any species of stingless bee were recorded in the dry season (especially December 2004-January 2005). The small species, *T. ventralis* was exceptional in that the highest number of pollen types was recorded in October 2004 (7 types). The numbers of pollen types collected by *T. ventralis* declined over the November-February period with the result that the numbers for each month in the dry season were only slightly higher than those in the wet season.

LMDF: The pollen types collected by each species of stingless bee in LMDF fluctuated somewhat inconsistently during the study period. In general, numbers of types of pollen were greater during the dry season and declined as the wet season

progressed. The highest numbers of types of pollen for any species were recorded in the dry season (in November 2004 and February 2005).

DEF: The data for DEF comprises the seasonal changes in the number of pollen types collected by foragers from two colonies of *T. apicalis*. The highest number of pollen types collected by *T. apicalis* from were recorded in January and February 2005 (9 and 11 types respectively). The numbers of pollen types for each month in the dry season were slightly higher than those in the wet season. (Figure 44)

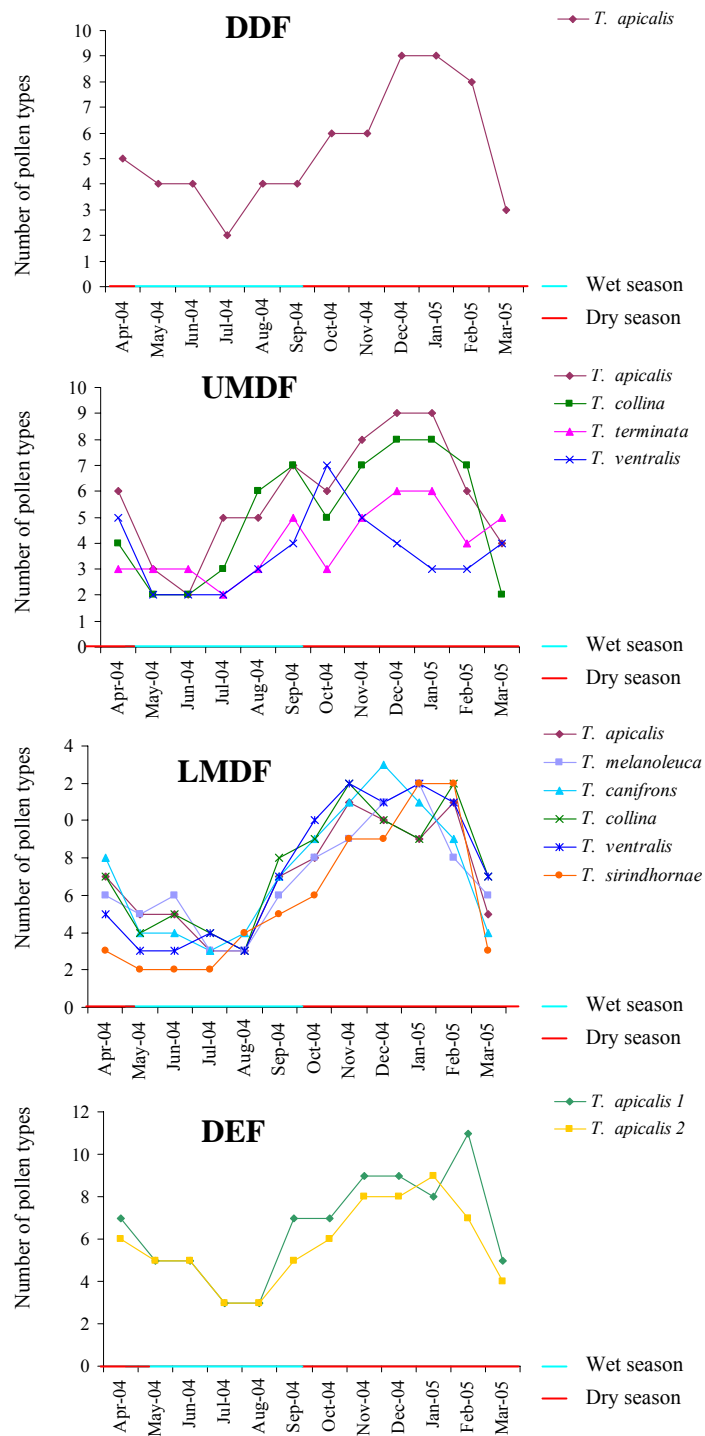


Figure 44 The seasonal changes in the number of pollen types collected by stingless bees in four types of forest.

Figure 45 aggregates the pollen type data and shows the numbers of pollen types that were collected by stingless bees in the four types of forest. LMDF had the highest number of plant species (36 pollen types) followed by UMDF, DDF and DEF, (32, 27 and 16 respectively).

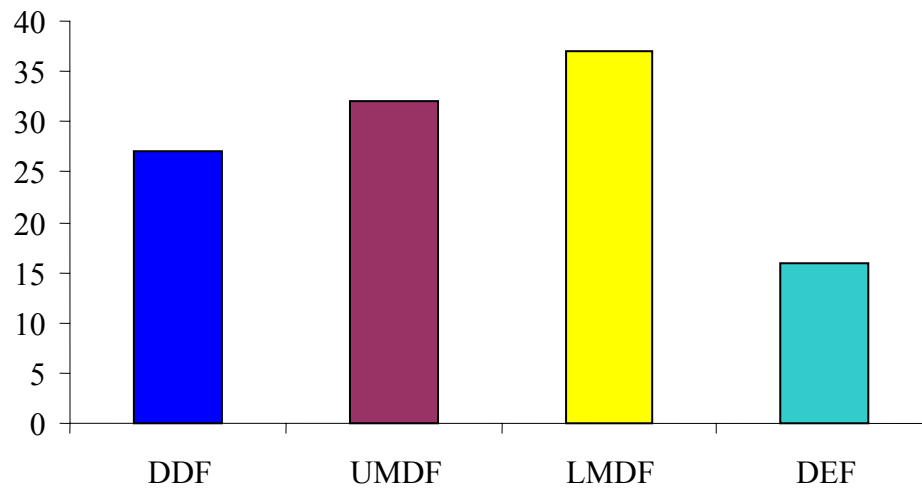


Figure 45 The total number of pollen types collected by stingless bees in four types of forest.

Figure 46 shows the numbers of pollen types collected by the different stingless bee species in each of the four types of forest.

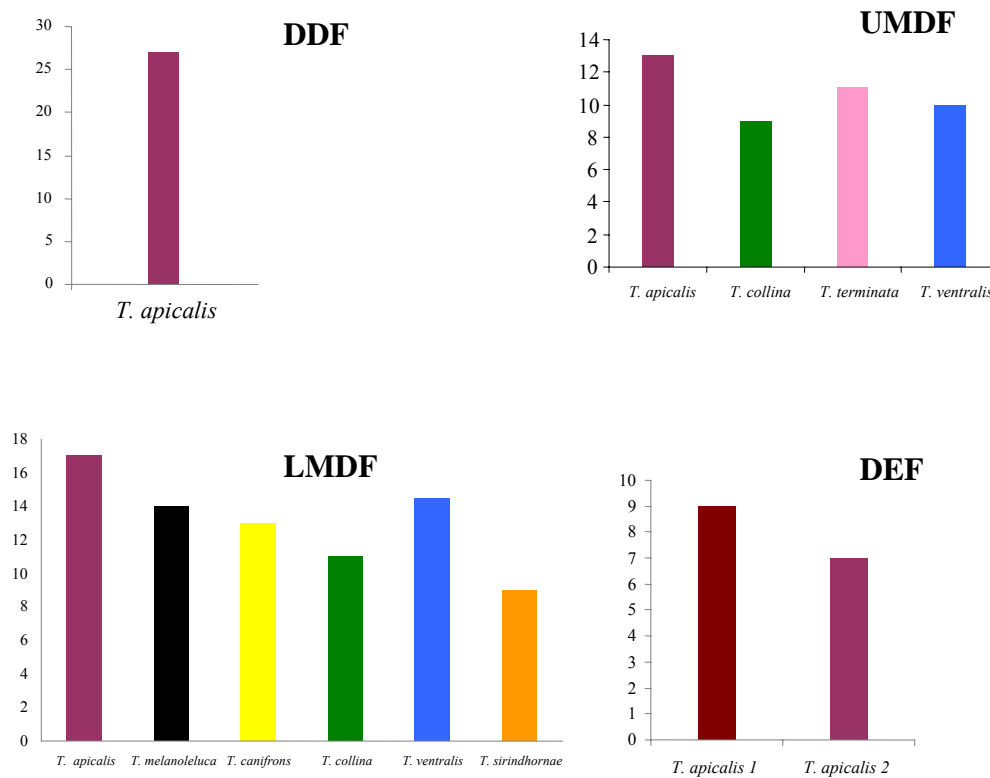


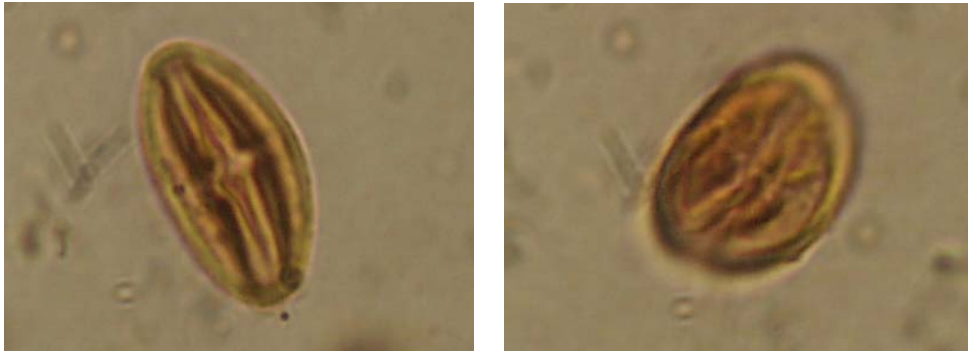
Figure 46 Number of pollen types collected by stingless bees species in four types of forest.

Figures 47 - 50 show the pollen of 112 plant species (representing 38 families of plants) collected by stingless bees from the four types of forest.

Pollen collected by stingless bees in dry dipterocarp forest (DDF)

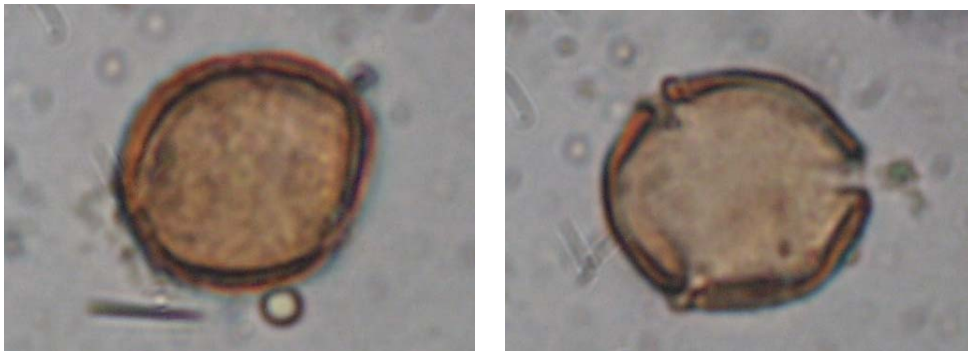
T. apicalis only was observed in this forest type. Pollen analysis showed that *T. apicalis* workers were able to collect pollen from a total of 27 plant species. Of these plant species, 16 could be identified to family (14 families represented): *Lithocarpus thomsonii* (Miq.) Rehder (Fagaceae); *Dillenia parviflora* and *Dillenia* sp. (Dileniaceae); *Hopea* sp. (Dipterocarpaceae); Euphorbiaceae; Caesalpiniaceae (3 species); Fabaceae (2 species); Verbenaceae (2 species); Phormiaceae (1 species); Acanthaceae (3 species); and Robiaceae (1 species) (Figure 47)

1) *Lithocarpus thomsonii* (Miq.) Rehder **Family Fagaceae**



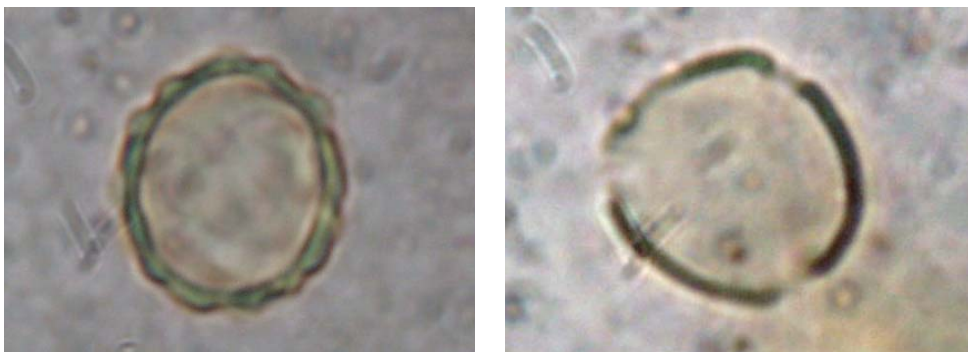
Grain diameter (equatorial axis 29 microns, polar 15 microns)

2) *Dillenia* sp. **Family Dilleniaceae**



Grain diameter (equatorial axis 17.5 microns, polar axis 17.5 microns)

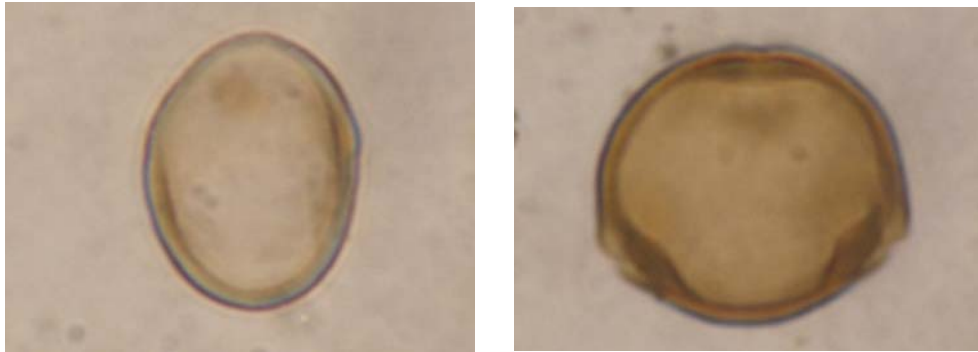
3) *Dillenia parviflora* **Family Dilleniaceae**



Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

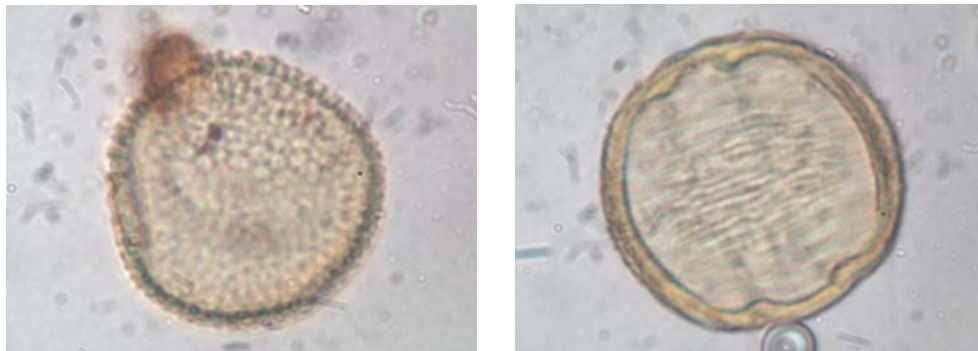
Figure 47 Pollen types collected by stingless bee from DDF.

4) *Hopea* sp. **Family Dipterocarpaceae**



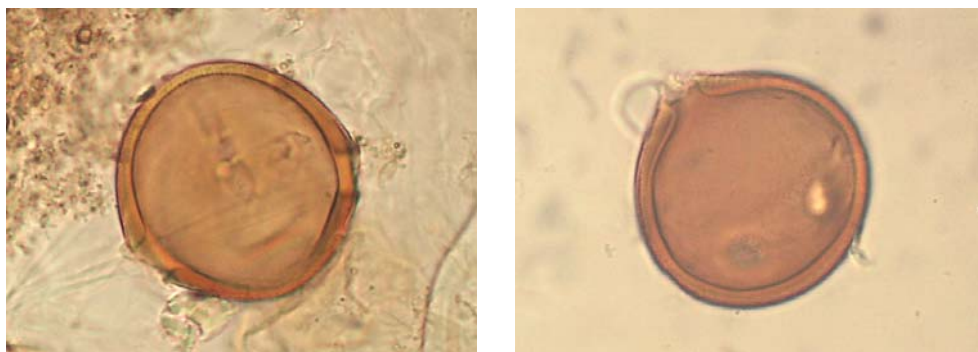
Grain diameter (equatorial axis 29 microns, polar axis 27 microns)

5) **Family Euphorbiaceae**



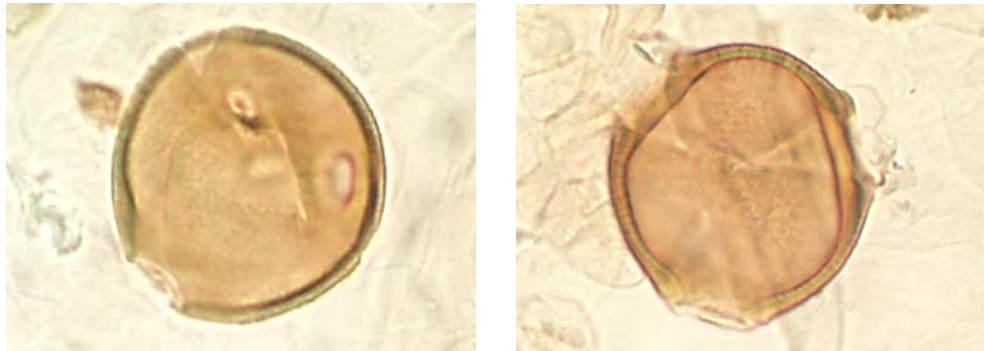
Grain diameter (equatorial axis 27 microns, polar axis 31 microns)

6) **Family Caesalpinaceae**



Grain diameter (equatorial axis 57.5 microns, polar axis 50 microns)

Figure 47 (Continued)

7) Family Fabaceae

Grain diameter (equatorial axis 40 microns, polar axis 40 microns)

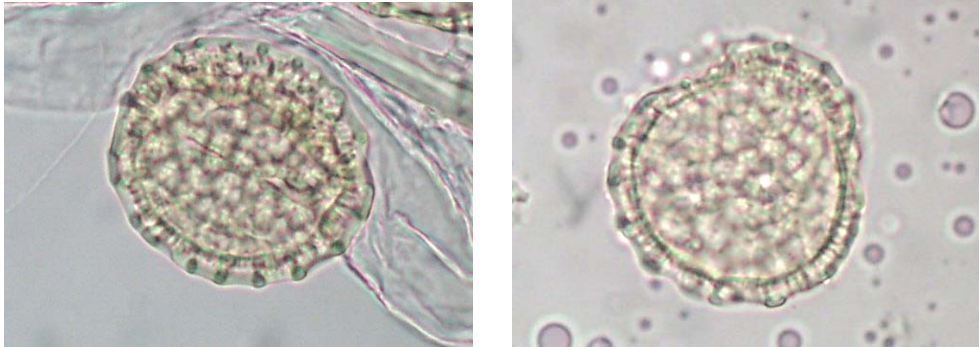
8) Family Verbenaceae

Grain diameter (polar axis 125 microns)

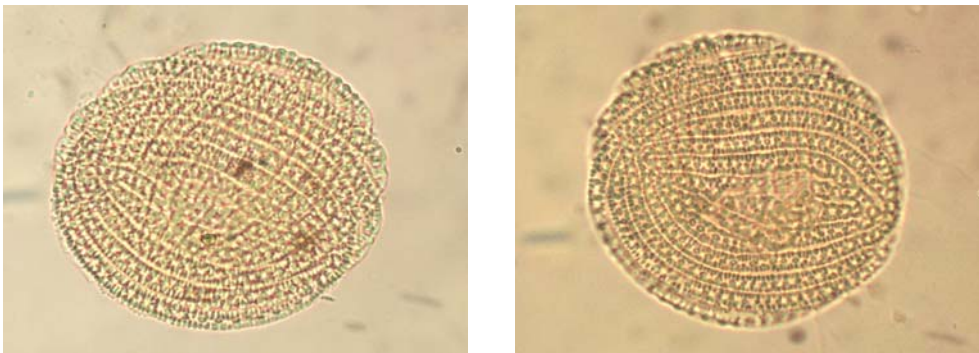
9) Family Phormianae

Grain diameter (equatorial axis 70 microns, polar axis 62.5 microns)

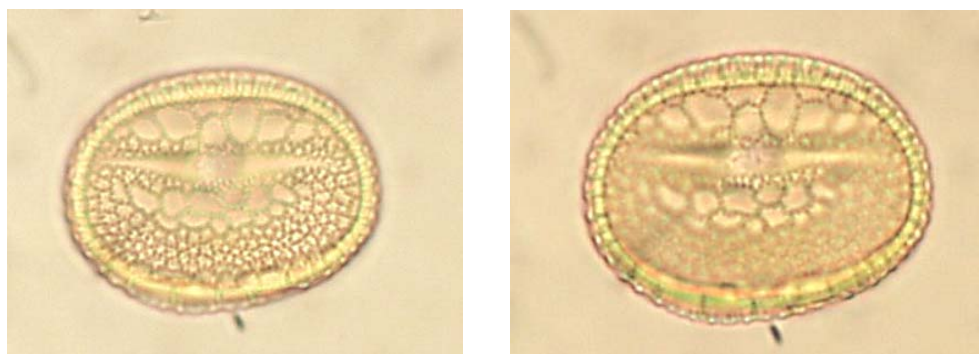
Figure 47 (Continued)

10) Family Caesalpiaceae

Grain diameter (equatorial axis 50 microns, polar axis 50 microns)

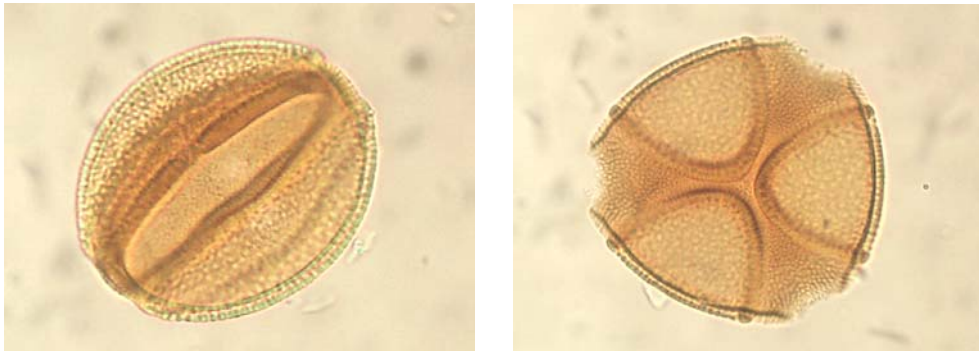
11) Family Acanthaceae

Grain diameter (equatorial axis 70 microns, polar axis 80 microns)

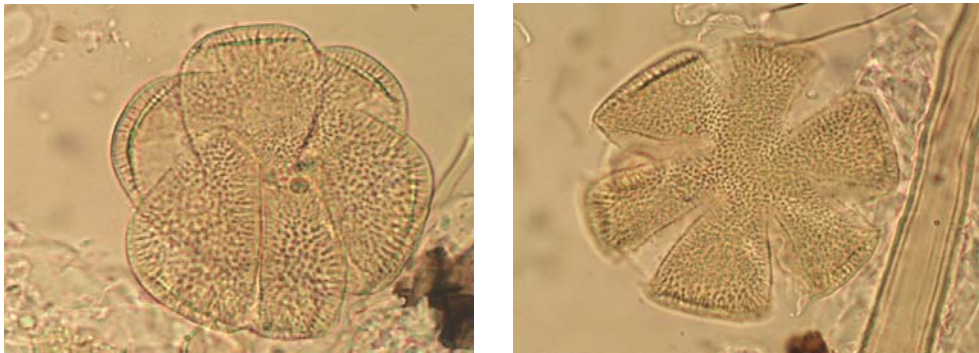
12) Family Acantraceae

Grain diameter (equatorial axis 55 microns, polar axis 37.5 microns)

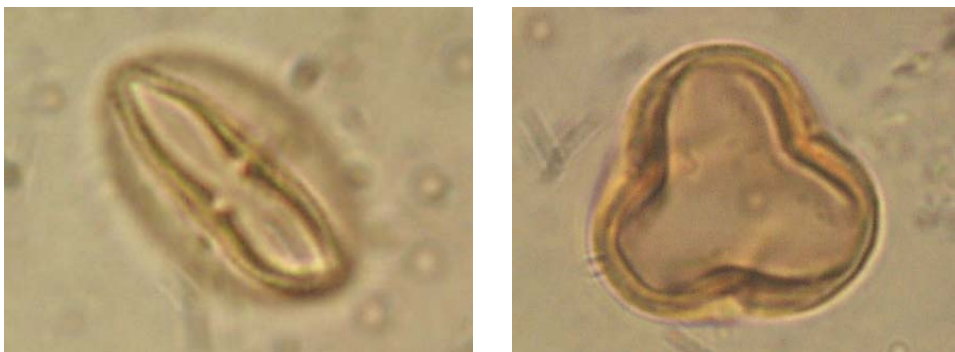
Figure 47 (Continued)

13) Family Caesalpiaceae

Grain diameter (equatorial axis 75 microns, polar axis 65 microns)

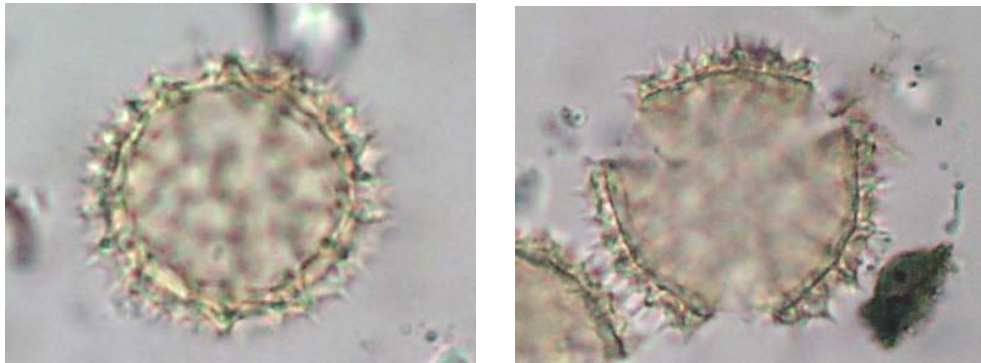
14) Family Verbenaceae

Grain diameter (equatorial axis 70 microns, polar axis 80 microns)

15) Family Euphorbiaceae

Grain diameter (equatorial axis 20 microns, polar axis 17.5 microns)

Figure 47 (Continued)

16) Family Fabaceae

Grain diameter (equatorial axis 37.5 microns, polar axis 37.5 microns)

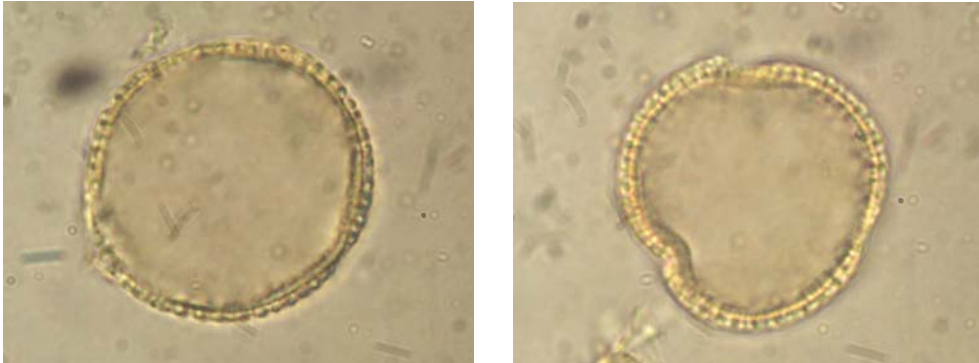
17) Family Acanthaceae

Grain diameter (equatorial axis 15 microns, polar axis 27 microns)

18) Family Euphorbiaceae

Grain diameter (equatorial axis 40 microns, polar axis 27 microns)

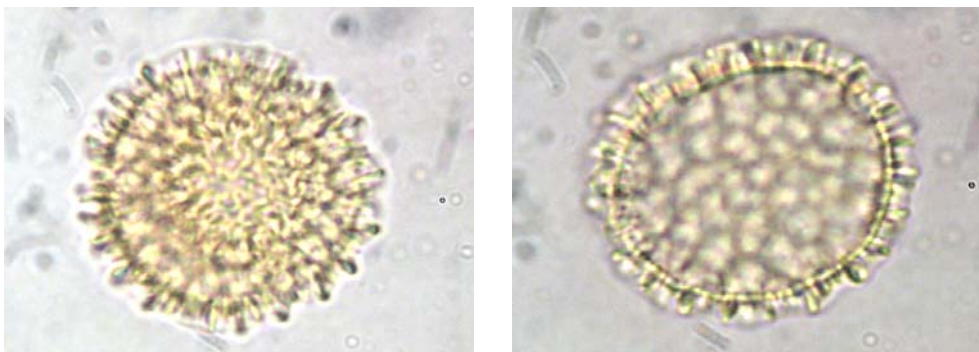
Figure 47 (Continued)

19) Family Rubiaceae

Grain diameter (equatorial axis 20 microns, polar axis 17.5 microns)

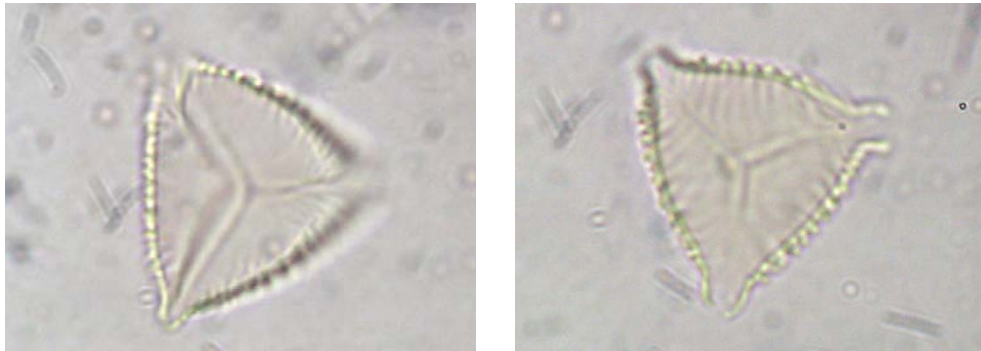
20) Unknown 1

Grain diameter (equatorial axis 57.5 microns, polar axis 57.5 microns)

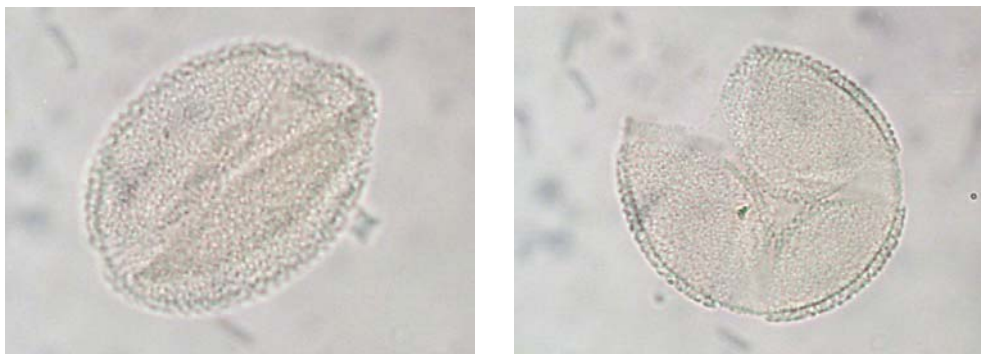
21) Unknown 2

Grain diameter (equatorial axis 30 microns, polar axis 30 microns)

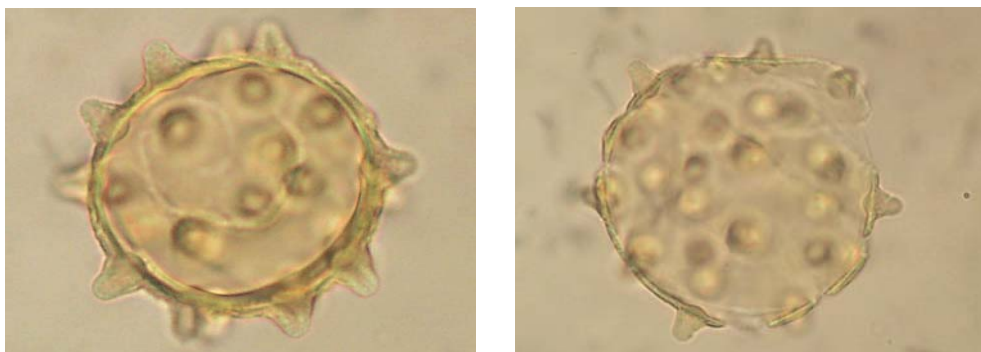
Figure 47 (Continued)

22) Unknown 3

Grain diameter (equatorial axis 50 microns, polar axis 50 microns)

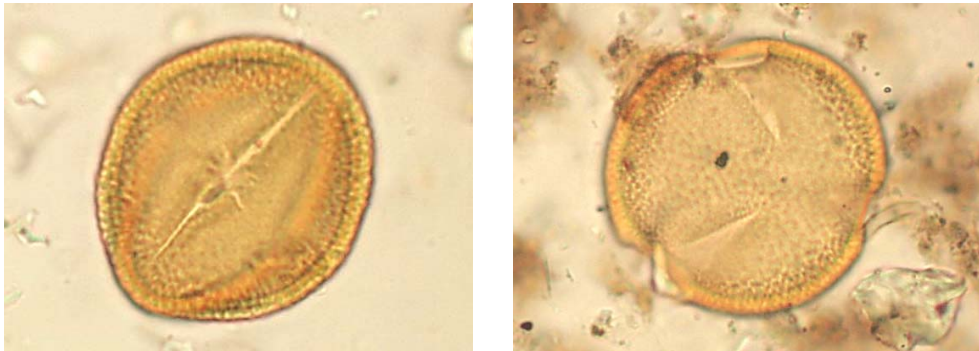
23) Unknown 4

Grain diameter (equatorial axis 50 microns, polar axis 62.5 microns)

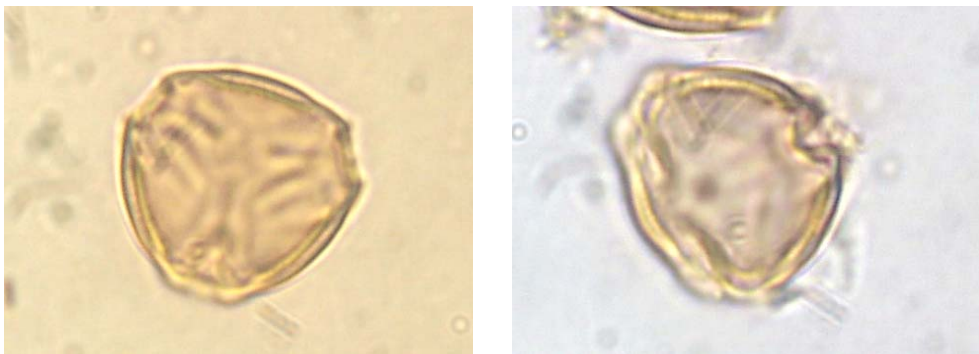
24) Unknown 5

Grain diameter (equatorial axis 75 microns, polar axis 75 microns)

Figure 47 (Continued)

25) Unknown 6

Grain diameter (equatorial axis 42.5microns, polar axis 60 microns)

26) Unknown 7

Grain diameter (equatorial axis18microns, polar axis20microns)

27) Unknown 8

Grain diameter (equatorial axis 33 microns, polar axis 33 microns)

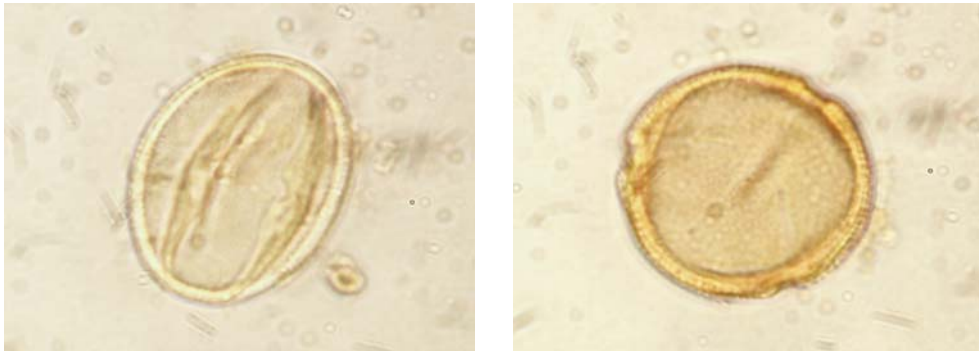
Figure 47 (Continued)

Pollen collected by stingless bees in upper mixed deciduous forest (UMDF)

In this forest, four species of bees were observed (*T. apicalis*, *T. collina*, *T. terminata* and *T. ventralis*). Most species collected similar pollen types except *T. apicalis* which was the only species that collected pollen from Verbenaceae.

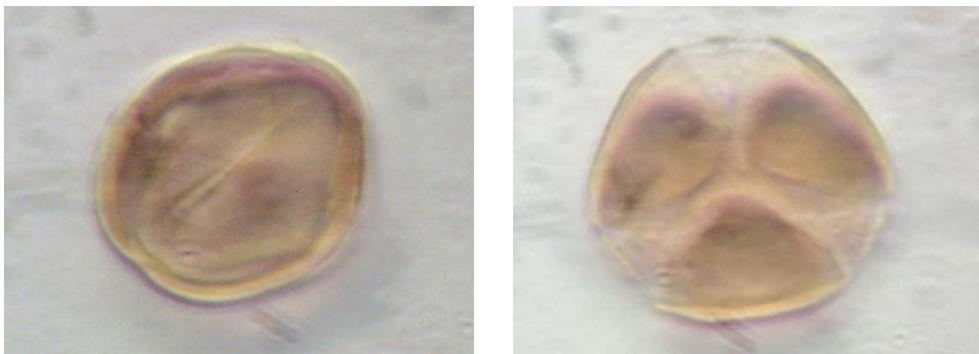
Pollen analysis showed that in UMDF stingless bee workers were able to collect pollen from a total of 47 plant species. Of these, 20 species representing 11 families could be identified: *Dalbergia oliveri* Gramble, *Dalbergia obovata* E. Mey, *Antidesma sootepense* Craib, *Vitex peduncularis* Wall. ex Schauer, *Melia azedarach* L., *Garuga pinnata* Roxb., *Gratoxylum formosum*, *Protium serratum* Engler. and representatives of the families Asteraceae, Caesalpiaceae, Mimosaceae, Asteraceae, Fabaceae, Euphorbiaceae, Lamiaceae, Meliaceae, Burseraceae and Guttiferae (Figure 48).

1) *Dalbergia oliveri* Gramble **Family Fabaceae**



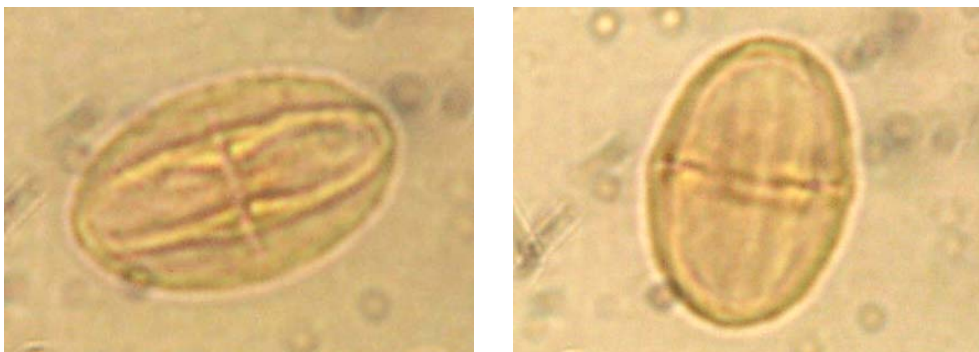
Grain diameter (polar axis 27.5 microns, equatorial axis 25 microns)

2) *Dalbergia obovata* E. Mey **Family Fabaceae**



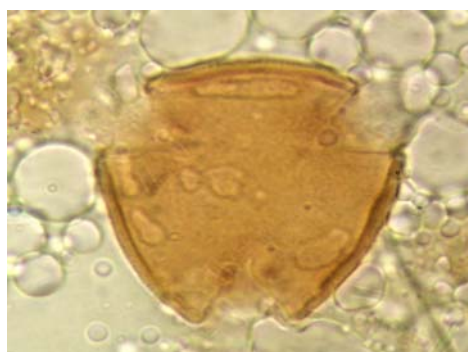
Grain diameter (equatorial axis 20 microns, polar axis 22.5 microns)

3) *Antidesma sootepense* Craib **Family Euphorbiaceae**



Grain diameter (equatorial axis 10 microns, polar axis 17.5 microns)

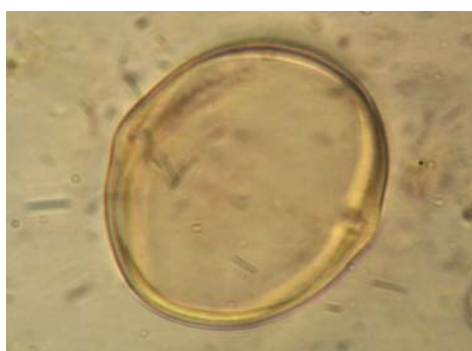
Figure 48 Pollen type collected by stingless bee from UMDP.

4) *Vitex peduncularis* Wall. ex Schauer**Family Lamiaceae**

Grain diameter (equatorial axis 37.5microns, polar axis 32.5 microns)

5) *Melia azedarach* L.**Family Meliaceae**

Grain diameter (equatorial axis 42 microns, polar axis 36 microns)

6) *Garuga pinnata* Roxb.**Family Burseraceae**

Grain diameter (equatorial axis 22.5 microns, polar axis 22.5 microns)

Figure 48 (Continued)

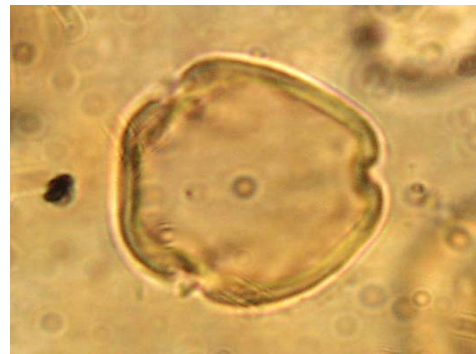
7) *Gratoxylum formosum*

Family Guttiferae



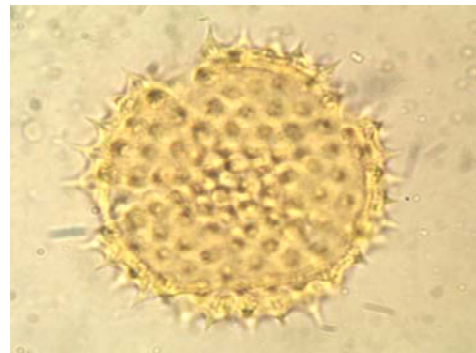
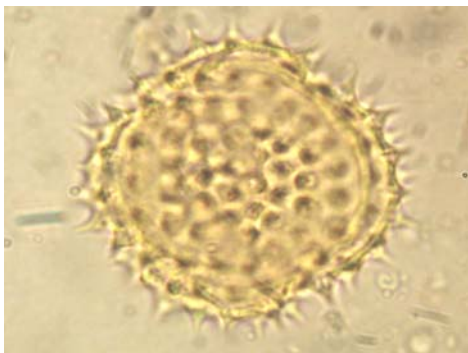
Grain diameter (equatorial axis 22.5 microns, polar axis 22.5 microns)

8) Family Burseraceae



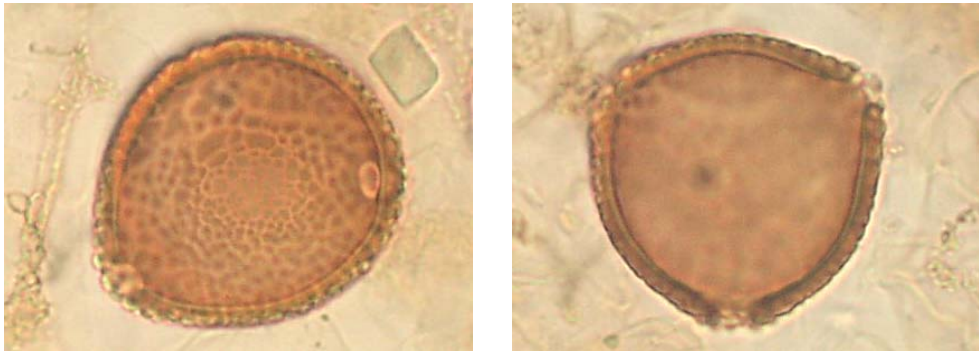
Grain diameter (equatorial axis 25 microns, polar axis 25 microns)

9) Family Asteraceae

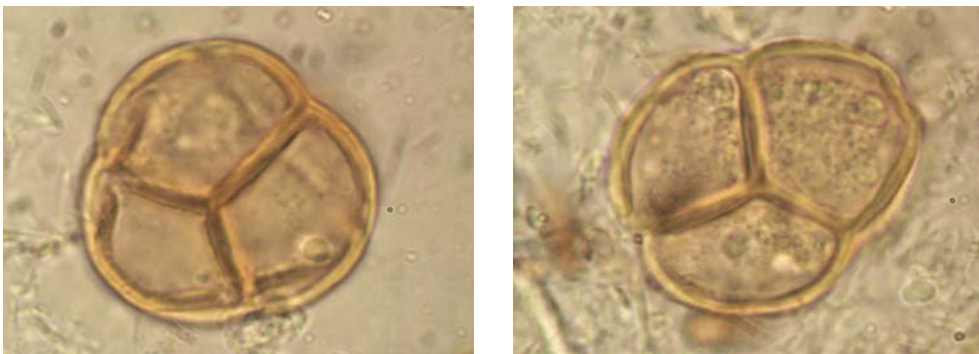


Grain diameter (equatorial axis 34 microns, polar axis 34 microns)

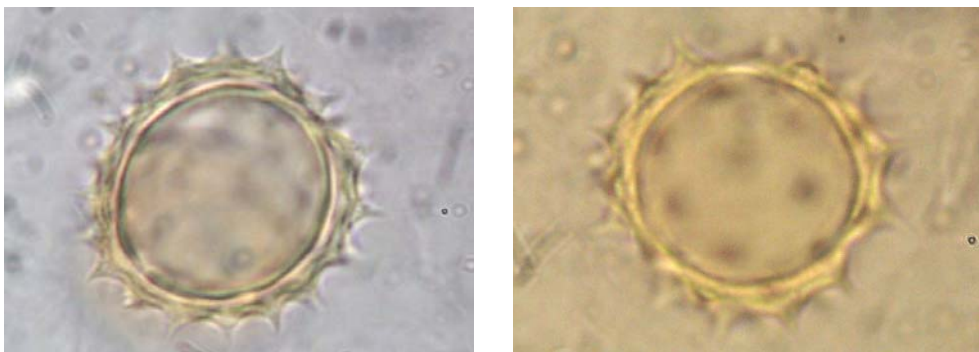
Figure 48 (Continued)

10) Family Caesalpiaceae

Grain diameter (equatorial axis 42.5microns, polar axis 50 microns)

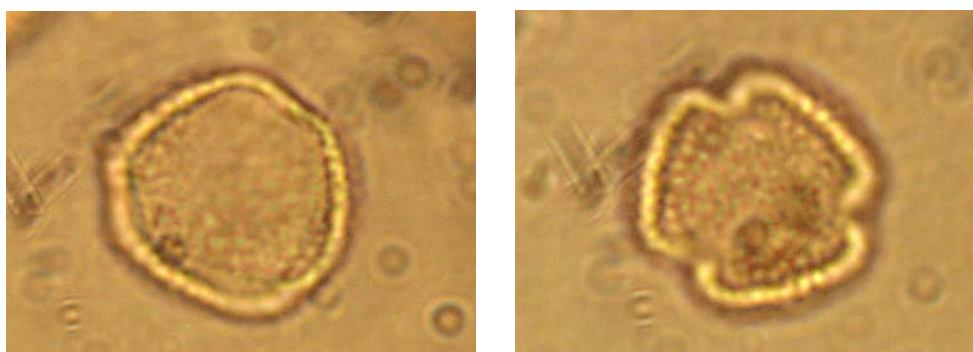
11) Family Mimosaceae

Grain diameter (equatorial axis 32 microns, polar axis 32 microns)

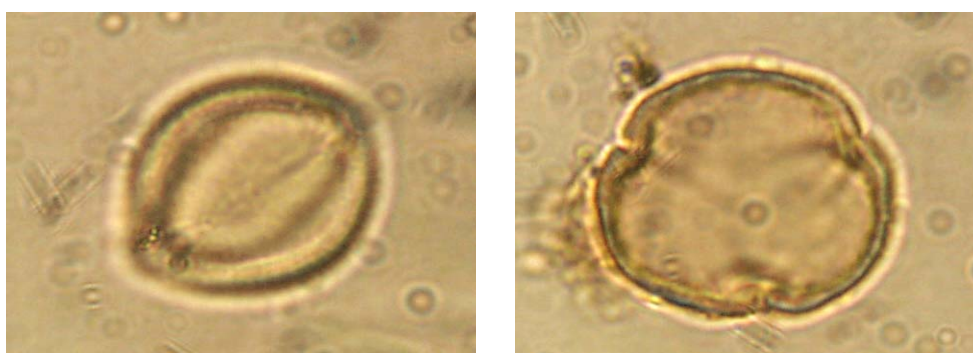
12) Family Asteraceae

Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

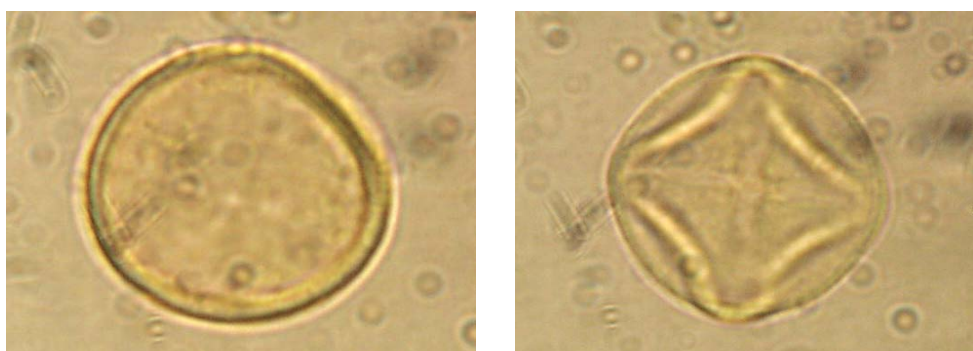
Figure 48 (Continued)

13) Unknown 9

Grain diameter (polar axis 35 microns, equatorial axis 29 microns)

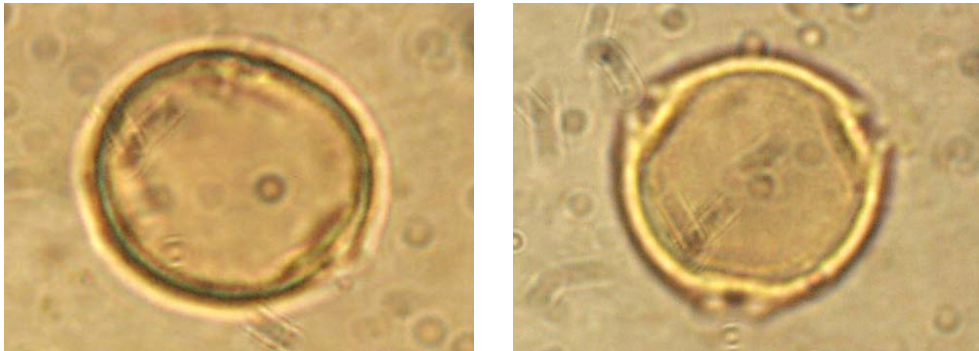
14) Unknown 10

Grain diameter (equatorial axis 19 microns, polar axis 17 microns)

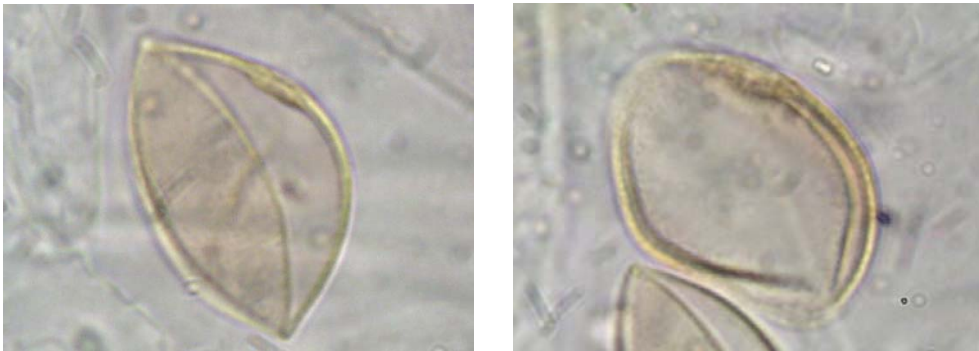
15) Unknown 11

Grain diameter (equatorial axis 22.5 microns, polar axis 22.5 microns)

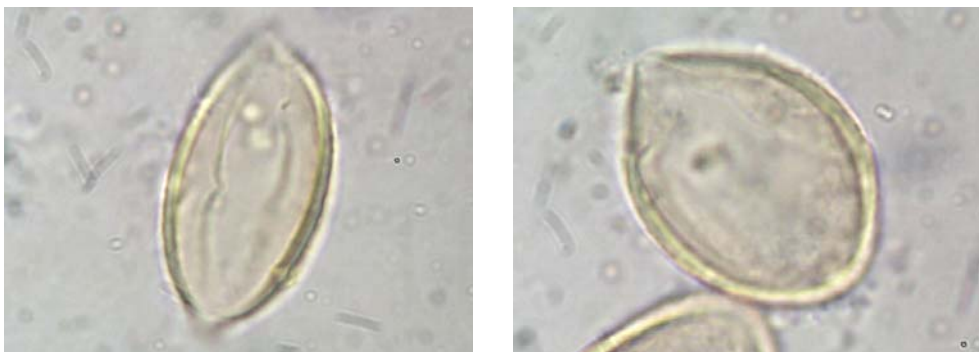
Figure 48 (Continued)

16) Unknown 12

Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

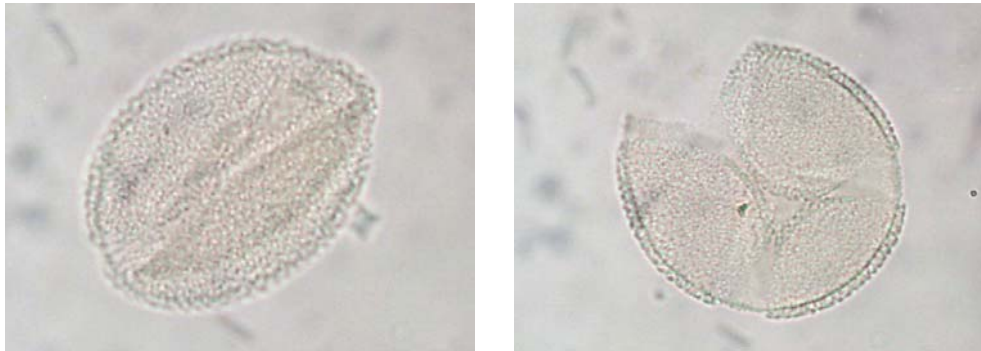
17) Unknown 13

Grain diameter (equatorial axis 30 microns, polar axis 17 microns)

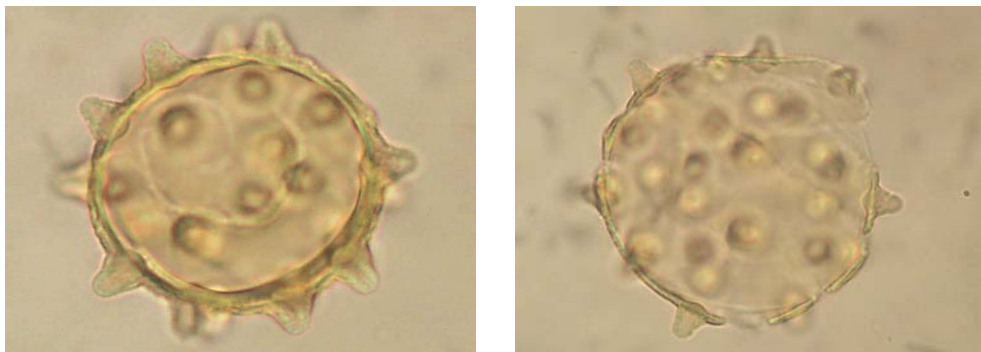
18) Unknown 14

Grain diameter (equatorial axis 32 microns, polar axis 19 microns)

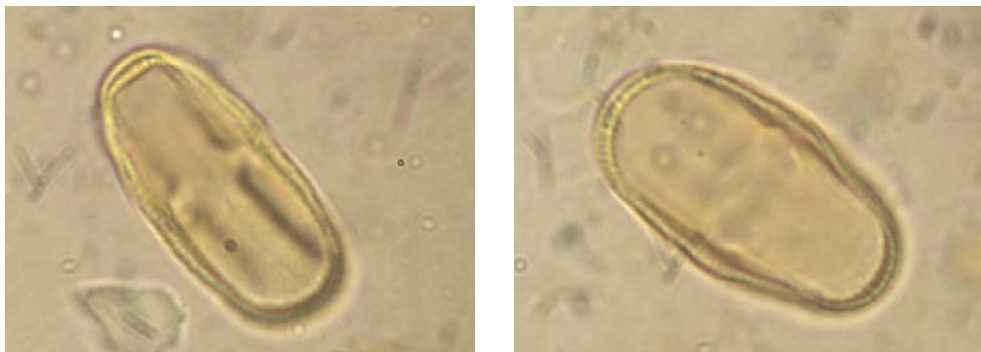
Figure 48 (Continued)

19) Unknown 15

Grain diameter (equatorial axis 50 microns, polar axis 62.5 microns)

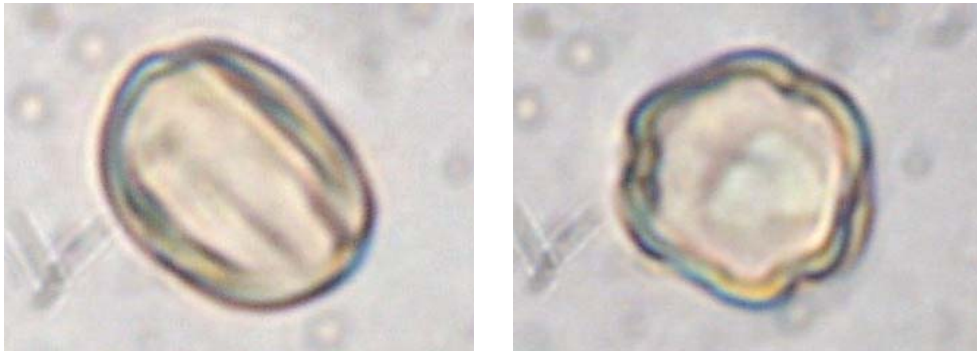
20) Unknown 16

Grain diameter (equatorial axis 75 microns, polar axis 75 microns)

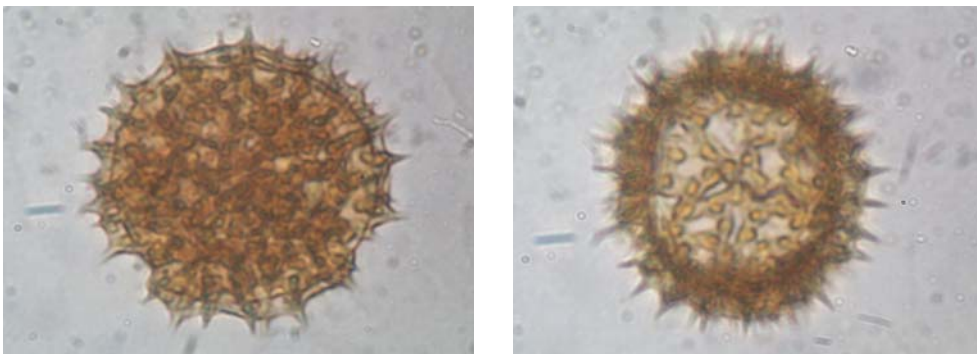
21) Unknown 17

Grain diameter (equatorial axis 15 microns, polar axis 27 microns)

Figure 48 (Continued)

22) Unknown 18

Grain diameter (equatorial axis 45 microns, polar axis 39 microns)

23) Unknown 19

Grain diameter (equatorial axis 45 microns, polar axis 45 microns)

24) Unknown 20

Grain diameter (equatorial axis 29 microns, polar axis 25 microns)

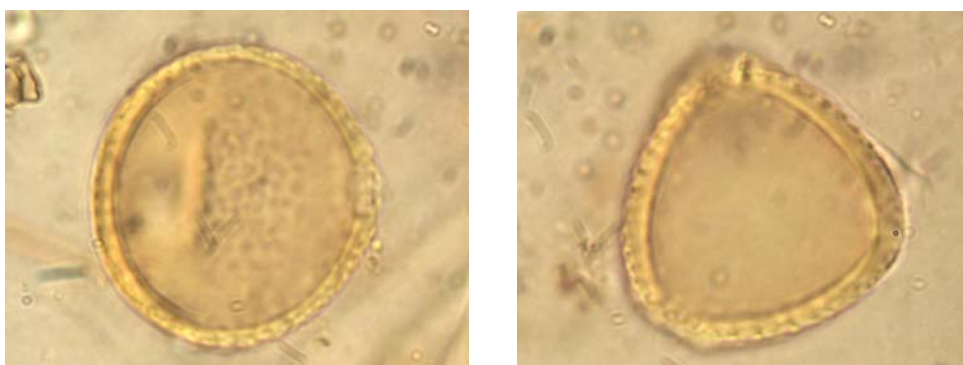
Figure 48 (Continued)

25) Unknown 21

Grain diameter (equatorial axis 24.5 microns, polar axis 23 microns)

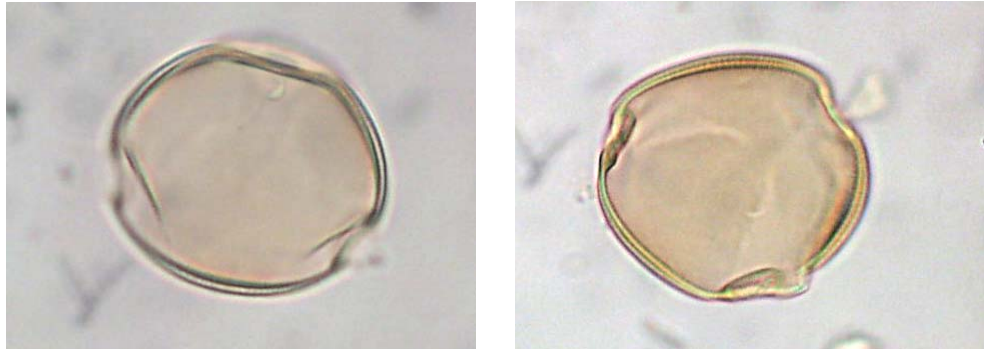
26) Unknown 22

Grain diameter (equatorial axis 45 microns, polar axis 45 microns)

27) Unknown 23

Grain diameter (equatorial axis 30 microns, polar axis 30 microns)

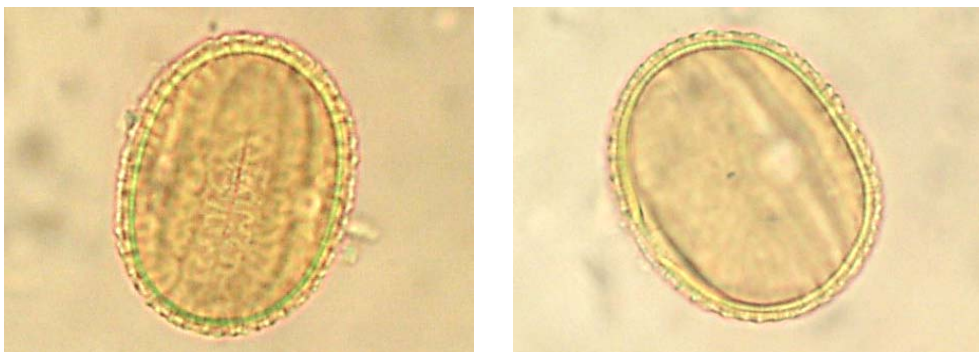
Figure 48 (Continued)

28) Unknown 24

Grain diameter (equatorial axis 37.5 microns, polar axis 45 microns)

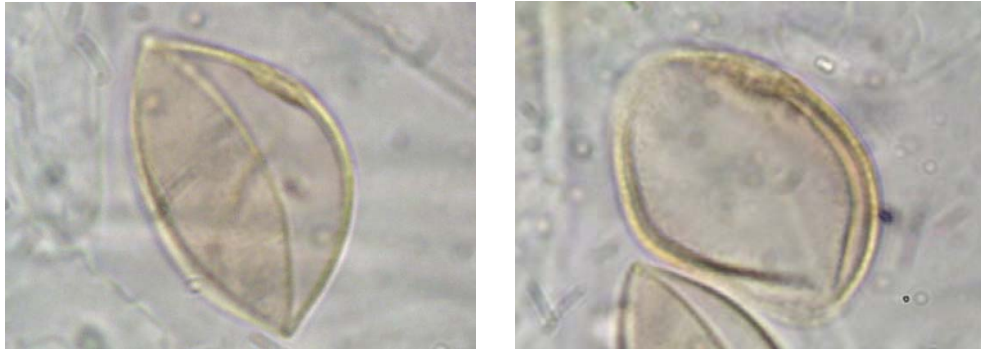
29) Unknown 25

Grain diameter (equatorial axis 24 microns, polar axis 24 microns)

30) Unknown 26

Grain diameter (equatorial axis 20 microns, polar axis 57.5 microns)

Figure 48 (Continued)

31) Unknown 27

Grain diameter (equatorial axis 30 microns, polar axis 17 microns)

32) Unknown 28

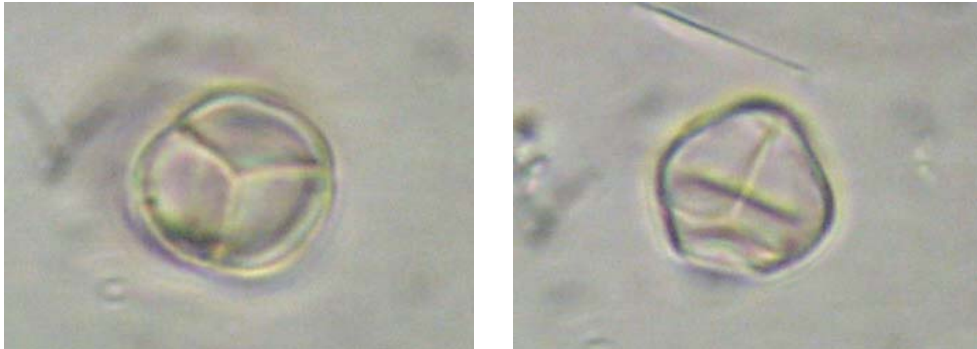
Grain diameter (equatorial axis 32 microns, polar axis 19 microns)

Figure 48 (Continued)

Pollen collected by stingless bees in lower mixed deciduous forest (LMDF)

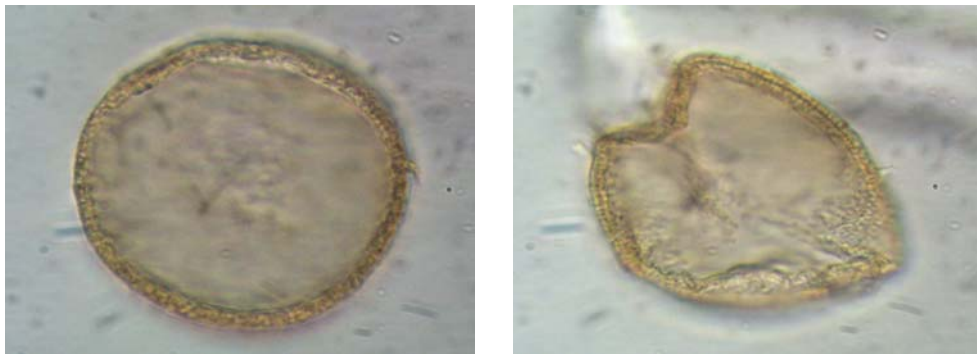
In this forest, six species of bees were observed (*T. apicalis*, *T. melanoleuca*, *T. canifrons*, *T. collina*, *T. ventralis* and *T. sirindhornae*). Most species collected similar pollen types. Pollen analysis showed that stingless bee workers were able to collect from a total of 44 plant species. Of these, 37 species could be identified to species (representing 29 families): *Mimosa pudica* (L.), *Annona squamosa* Linn., *Dimocarpus longan* Lour., *Parkia speciosa* Hassk., *Saraca indica* L., *Lagerstroemia tomentosa* C. Presl, *Muntingia calabura* L., *Elaeocarpus hygrophilus* Kurz., *Tectona grandis* L.f., *Schleichera oleosa* (Lour.) Oken, and representatives of the families Mimosaceae, Annonaceae, Sapindaceae, Mimosaceae, Caesalpiniaceae, Lythraceae, Elaeocarpaceae, Lamiaceae, Bignoniaceae, Hydrangeaceae, Compositae, Oleaceae, Verbenaceae, Araceae, Passifloraceae, Convolvulaceae, Caprifoliaceae, Capparidaceae, Tiliaceae, Costaceae, Salanaceae, Amaryllidaceae, Magnoliaceae, Convolvulaceae, Cucurbitaceae, Malvaceae (Figure 49).

1) *Mimosa pudica* (L.) **Family Mimosaceae**



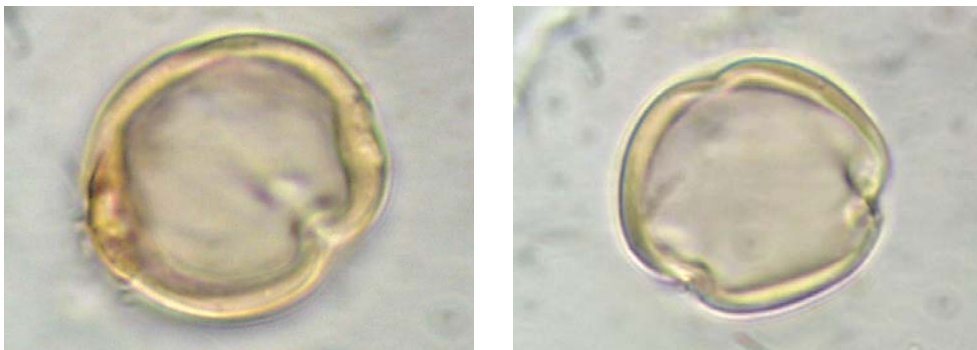
Grain diameter (equatorial axis 10 microns, polar axis 10 microns)

2) *Annona squamosa* Linn. **Family Annonaceae**



Grain diameter (equatorial axis 13 microns, polar axis 18 microns)

3) *Dimocarpus longan* Lour. **Family Sapindaceae**

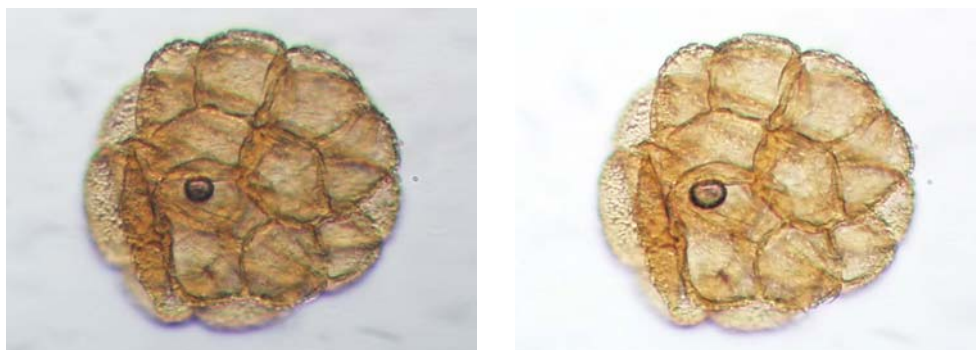


Grain diameter (equatorial axis 22.5 microns, polar axis 22.5 microns)

Figure 49 Pollen types collected by stingless bee from LMDF.

4) *Parkia speciosa* Hassk.

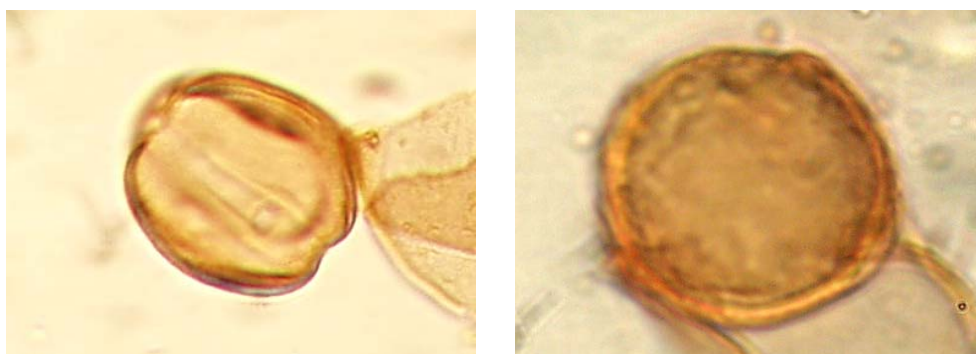
Family Mimosaceae



Grain diameter (equatorial axis 87.5 microns, polar axis 87.5 microns)

5) *Saraca indica* L.

Family Caesalpiniaceae



Grain diameter (equatorial axis 30 microns, polar axis 37.5 microns)

6) *Lagerstroemia tomentosa* C. Presl

Family Lythaceae

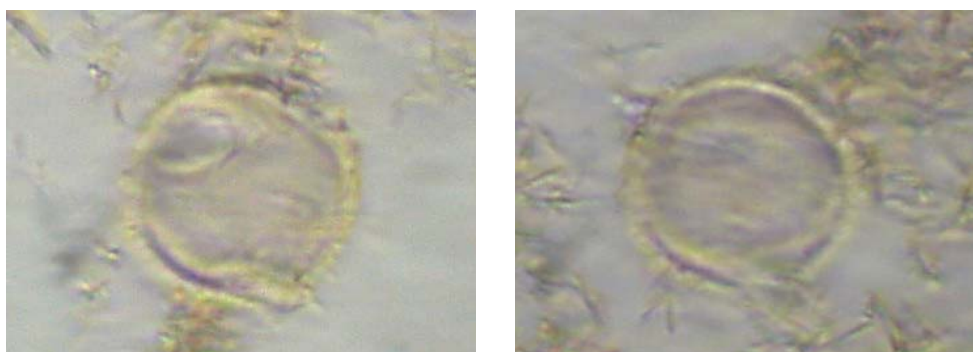


Grain diameter (equatorial axis 25 microns, polar axis 27.5 microns)

Figure 49 (Continued)

7) *Muntingia calabura* L.

Family Tiliaceae



Grain diameter (equatorial axis 12.5 microns, polar axis 12.5 microns)

8) *Elaeocarpus hygrophilus* Kurz.

Family Elaeocarpaceae



Grain diameter (equatorial axis 30 microns, polar axis 30 microns)

9) *Schleichera oleosa* (Lour.) Oken

Family Sapindaceae



Grain diameter (polar axis 32.5 microns)

Figure 49 (Continued)

10) *Tectona grandis* L.f.**Family Lamiaceae**

Grain diameter (equatorial axis 22 microns, polar axis 16 microns)

11) Family Bignoniaceae

Grain diameter (equatorial axis 50 microns, polar axis 45 microns)

12) Family Hydrangeaceae

Grain diameter (equatorial axis 55 microns, polar 47.5 microns)

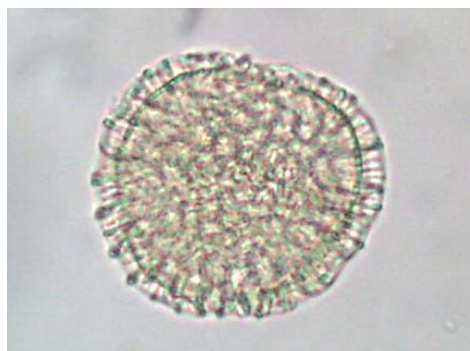
Figure 49 (Continued)

13) Family Compositae

Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

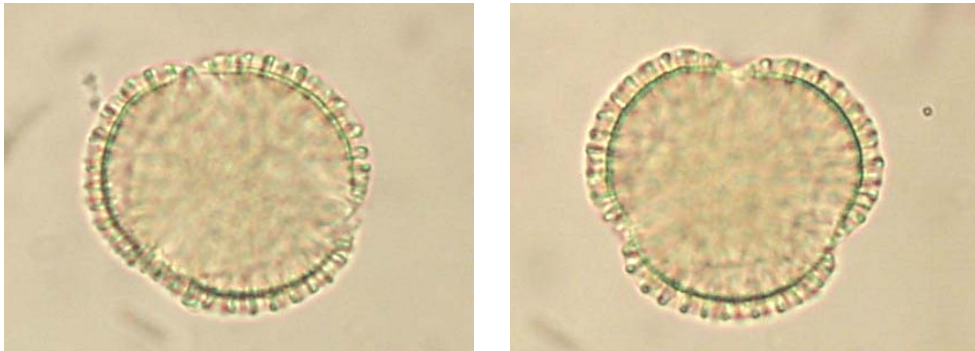
14) Family Verbenaceae

Grain diameter (equatorial axis 72.5 microns, polar axis 72.5 microns)

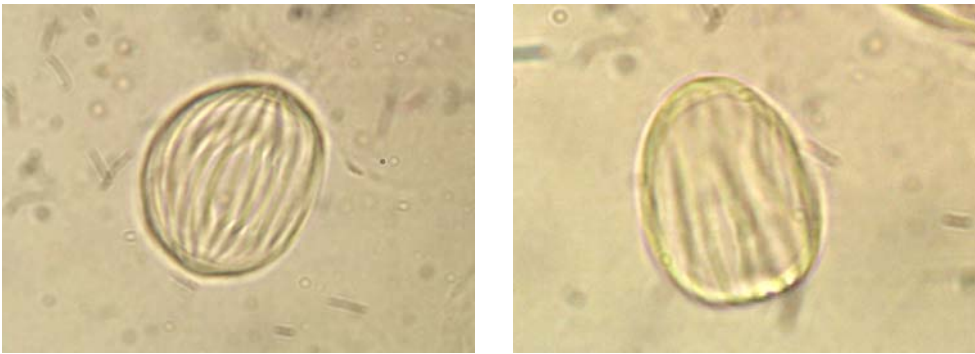
15) Family Oleaceae

Grain diameter (equatorial axis 45 microns, polar axis 45 microns)

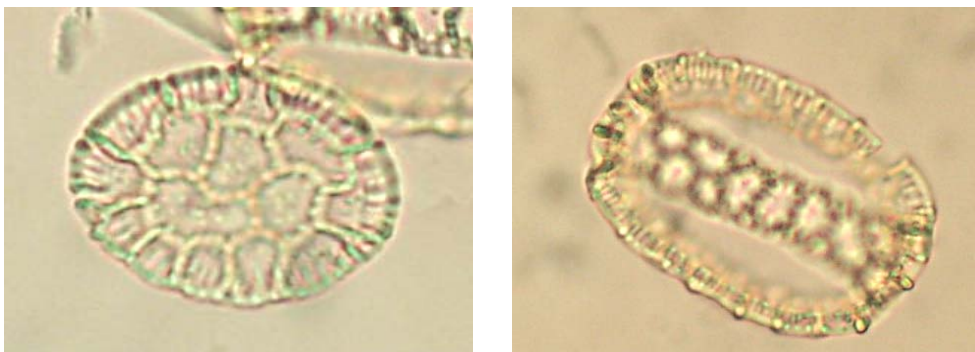
Figure 49 (Continued)

16) Family Oleaceae

Grain diameter (equatorial axis 50 microns, polar axis 50 microns)

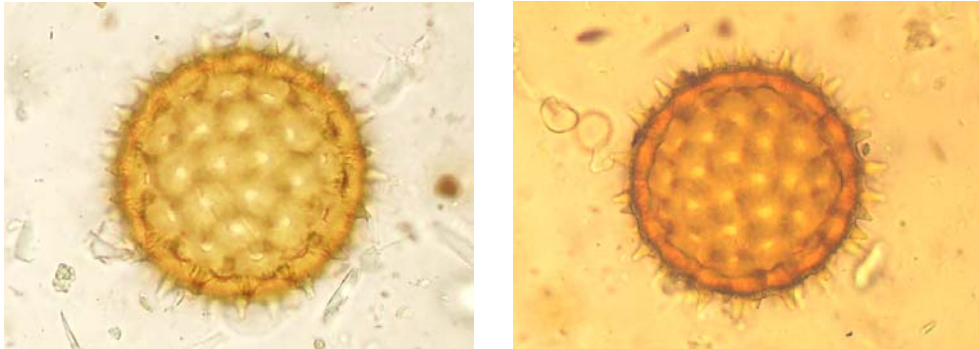
17) Family Araceae

Grain diameter (equatorial axis 25 microns, polar axis 16 microns)

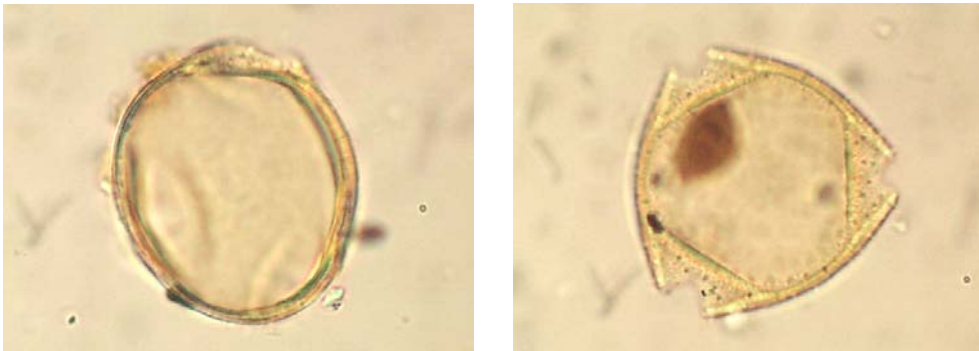
18) Family Passifloraceae

Grain diameter (equatorial axis 62.5 microns, polar axis 30 microns)

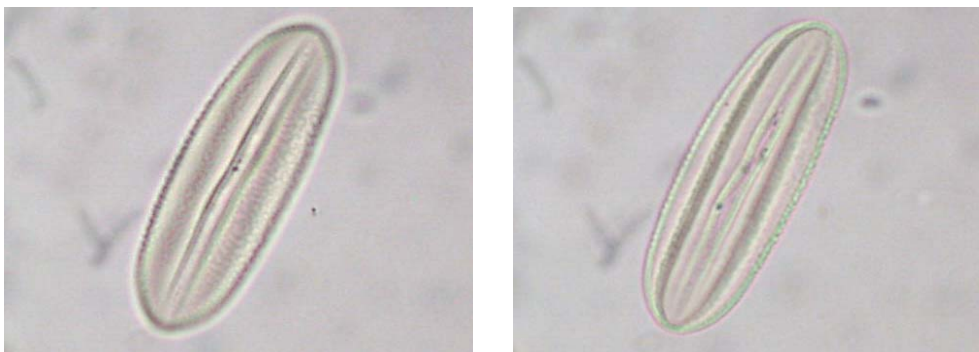
Figure 49 (Continued)

19) Family Convolvulaceae

Grain diameter (equatorial axis 55 microns, polar axis 55 microns)

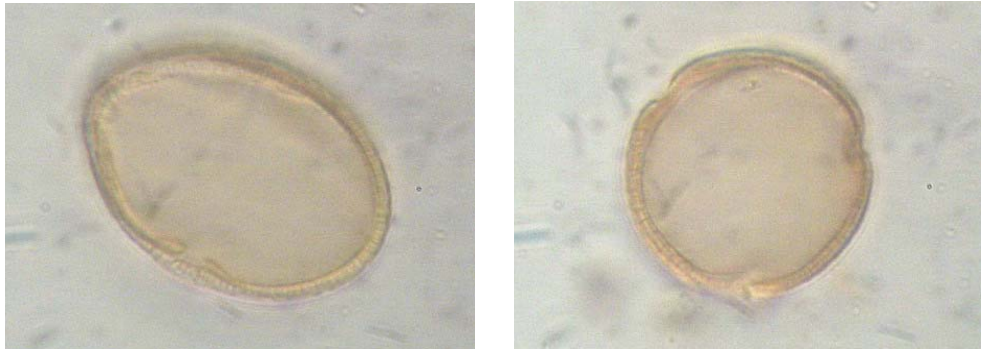
20) Family Caprifoliaceae

Grain diameter (equatorial axis 50 microns, polar axis 57.5 microns)

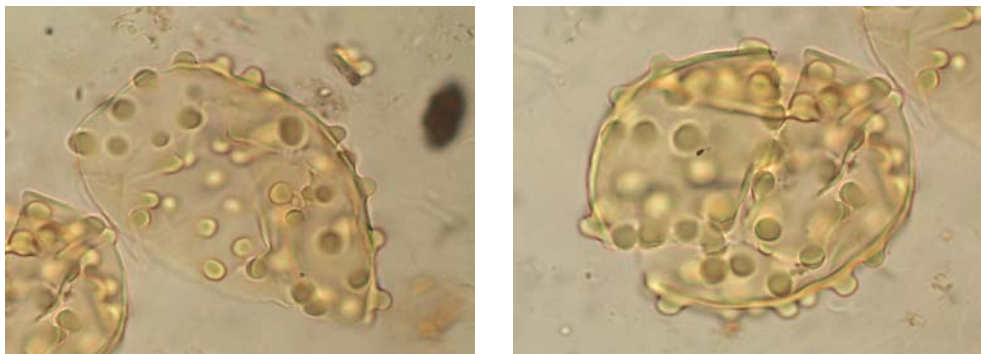
21) Family Capparidaceae

Grain diameter (equatorial axis 55 microns, polar axis 25 microns)

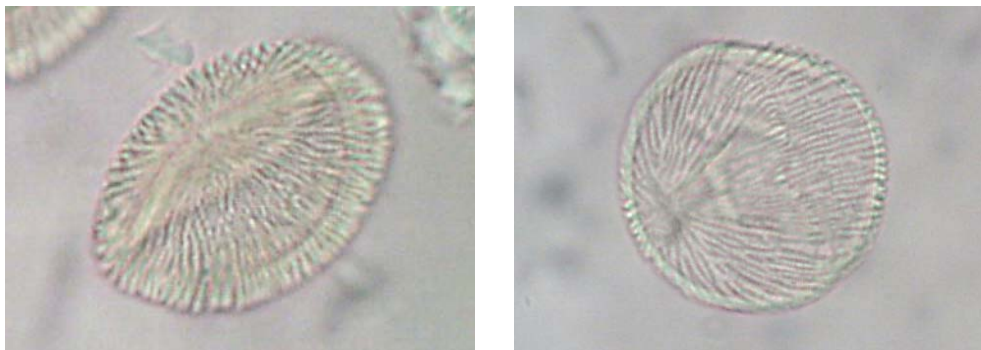
Figure 49 (Continued)

22) Family Tiliaceae

Grain diameter (equatorial axis 37.5 microns, polar axis 37.5 microns)

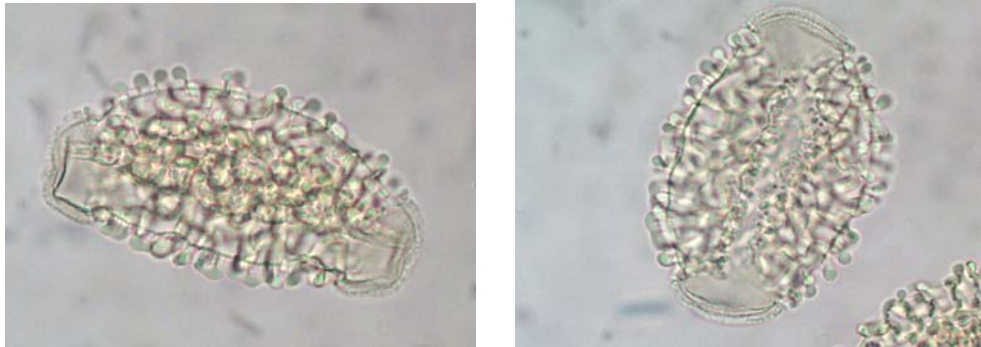
23) Family Costaceae

Grain diameter (equatorial axis 82.5microns, polar axis 80 microns)

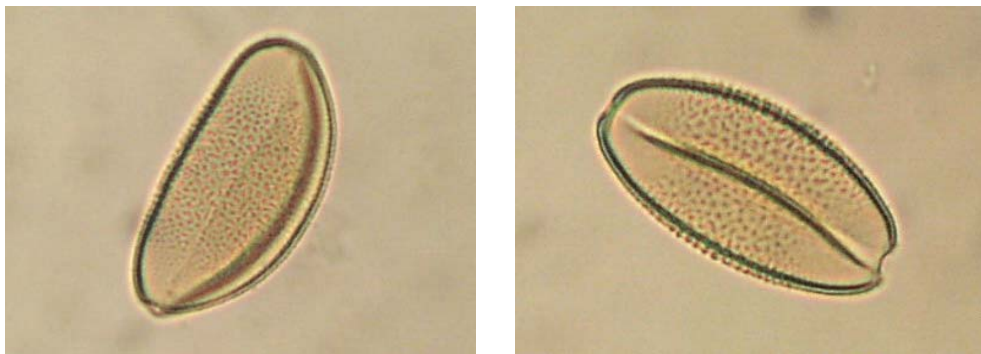
24) Family Salanaceae

Grain diameter (equatorial axis 42.5 microns, polar axis 35 microns)

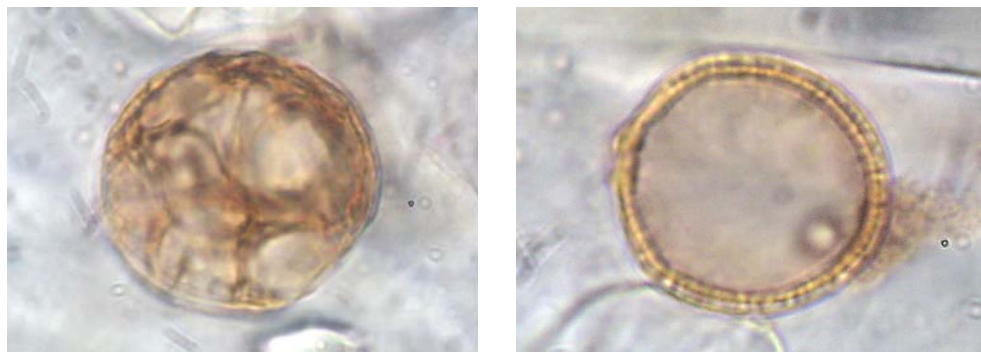
Figure 49 (Continued)

25) Family Amaryllidaceae

Grain diameter (equatorial axis 55 microns, polar axis 87.5 microns)

26) Family Amaryllidaceae

Grain diameter (equatorial axis 12.5 microns, polar axis 50 microns)

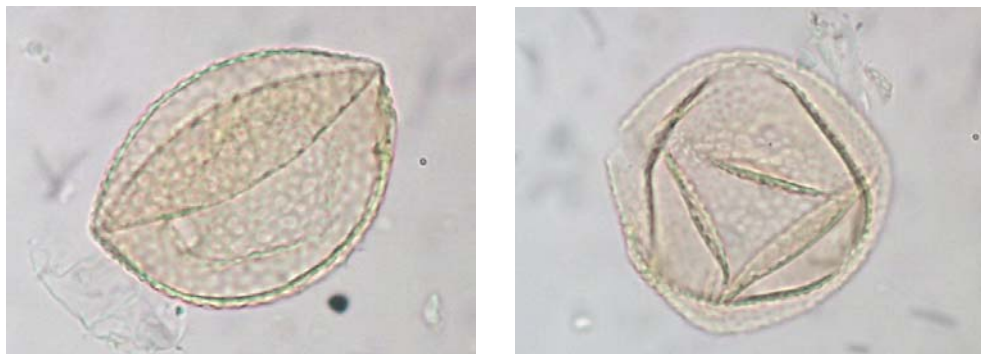
27) Family Magnoliaceae

Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

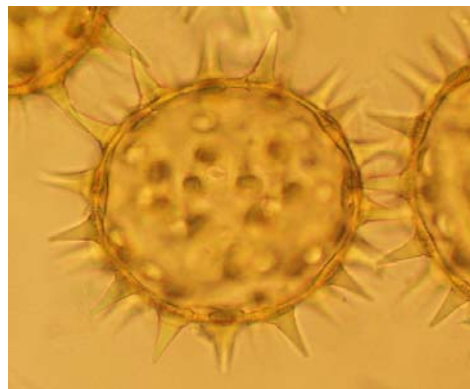
Figure 49 (Continued)

28) Family Convolvulaceae

Grain diameter (equatorial axis 37.5 microns, polar axis 20 microns)

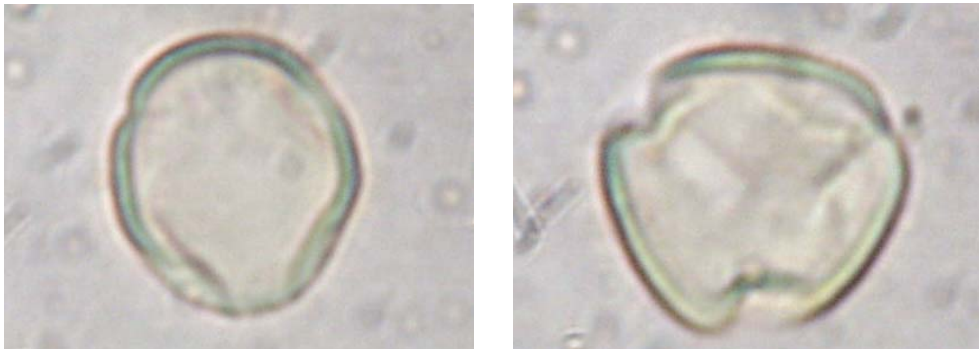
29) Family Cucurbitaceae

Grain diameter (equatorial axis 65 micron, polar axis 75microns)

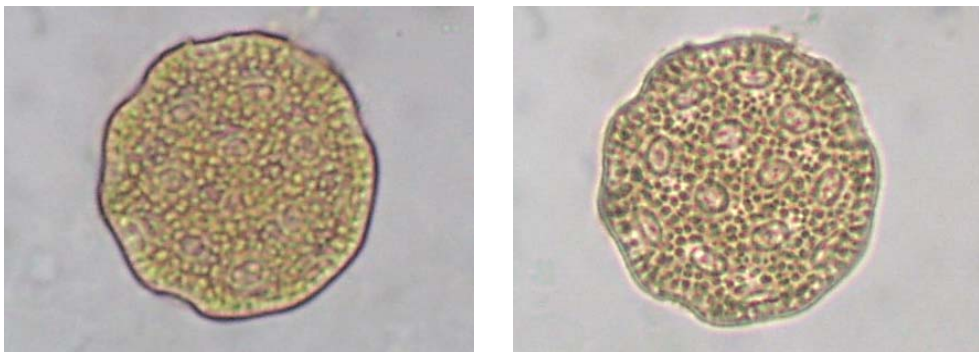
37) Family Malvaceae

Grain diameter (equatorial axis 150 microns, polar axis 150 microns)

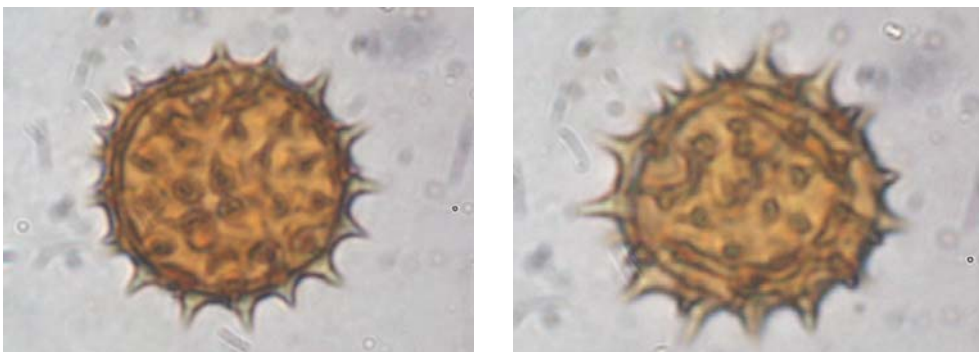
Figure 49 (Continued)

31) Unknown 29

Grain diameter (equatorial axis 22.5 microns, polar axis 23 microns)

32) Unknown 30

Grain diameter (equatorial axis 36 microns, polar axis 36 microns)

33) Unknown 31

Grain diameter (equatorial axis 45 microns, polar axis 45 microns)

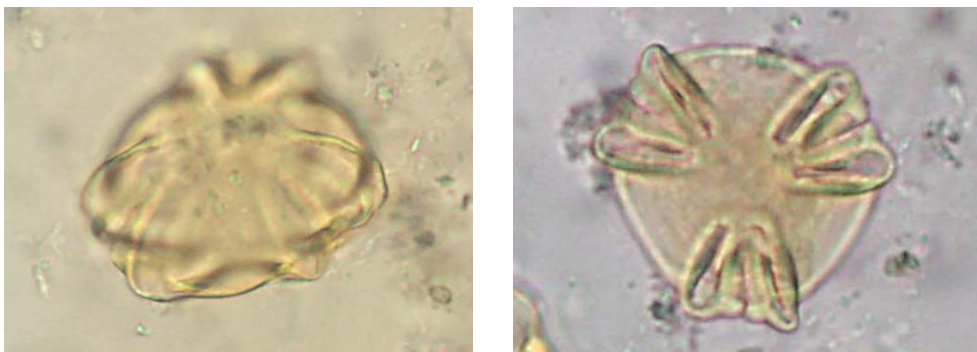
Figure 49 (Continued)

34) Unknown 32

Grain diameter (equatorial axis 21 microns, polar axis 21 microns)

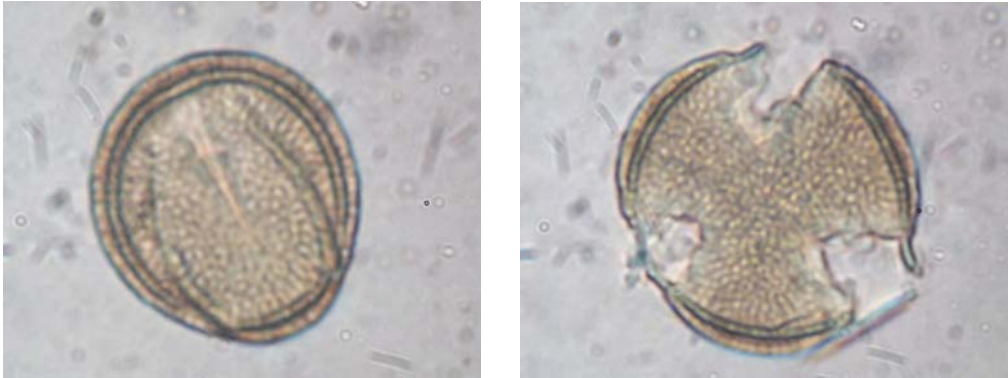
35) Unknown 33

Grain diameter (equatorial axis 29 microns, polar axis 27 microns)

36) Unknown 34

Grain diameter (equatorial axis 30 microns, polar axis 57.5 microns)

Figure 49 (Continued)

37) Unknown 35

Grain diameter (equatorial axis 35 microns, polar axis 27.5 microns)

Figure 49 (Continued)

Pollen collected by stingless bee in dry evergreen forest (DEF)

In this forest two nests of one species were observed (*T. apicalis* nest 1 and *T. apicalis* nest 2). Pollen analysis showed that in DEF *T. apicalis* workers were able to collect from a total of 21 plant species. Of these, 16 species (representing 10 families) could be identified: Caesalpiniaceae, Araceae, Labiatae, Compositae, Thunbergiaceae, Euphorbiaceae, Caesalpiniaceae, Mimosaceae and Asteraceae (Figure 50)

1) Family Caesalpiniaceae



Grain diameter (equatorial axis 30 microns, polar axis 30 microns)

2) Family Araceae

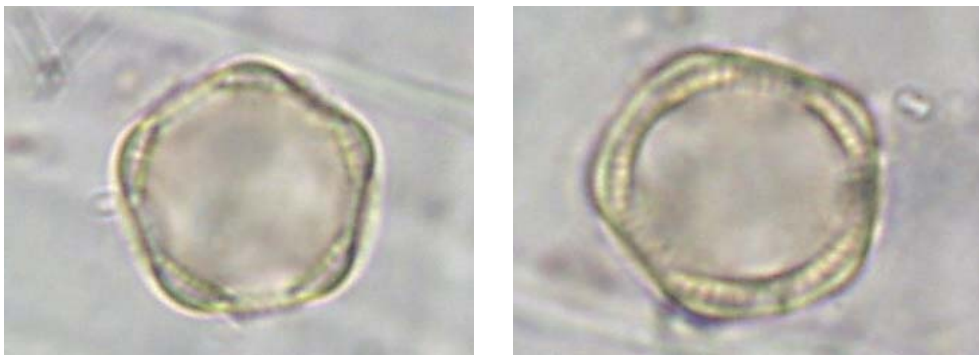


Grain diameter (equatorial axis 30 microns, polar axis 57.5 microns)

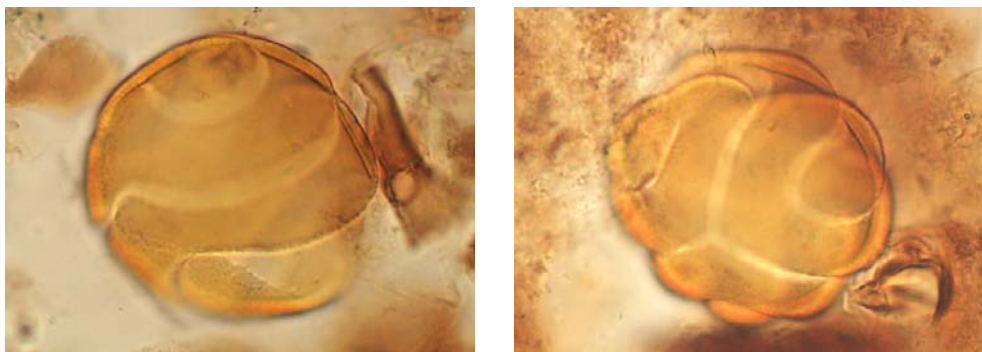
Figure 50 Pollen types collected by stingless bee from DEF.

3) Family Labiatae

Grain diameter (equatorial axis 25 microns, polar axis 30 microns)

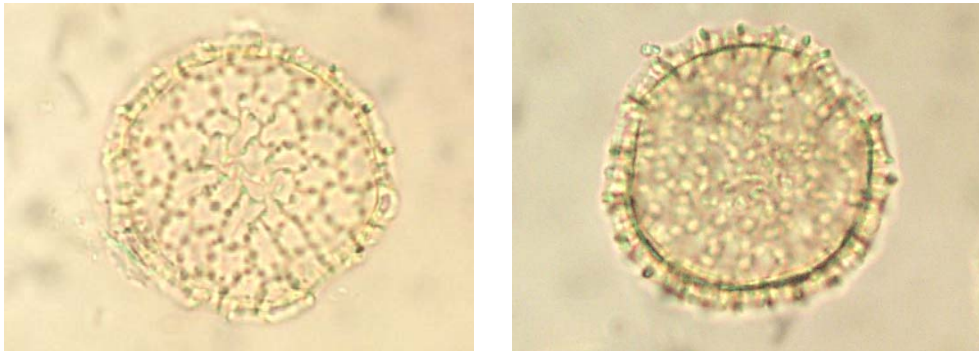
4) Family Compositae

Grain diameter (equatorial axis 14 microns, polar axis 14 microns)

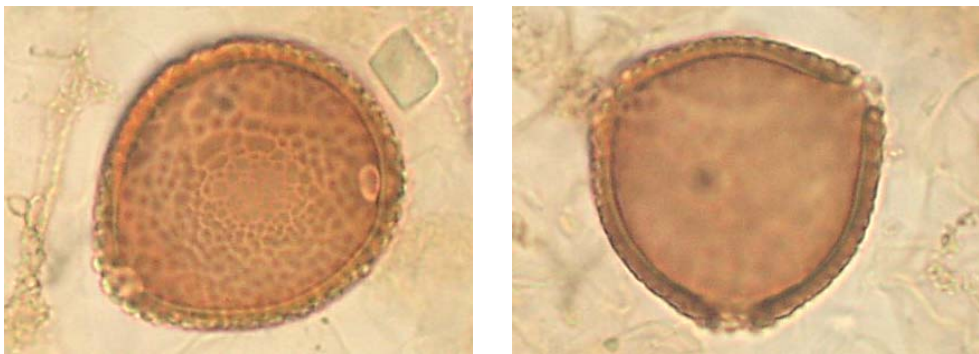
5) Family Thunbergiaceae

Grain diameter (equatorial axis 70 microns, polar axis 70 microns)

Figure 50 (Continued)

6) Family Euphorbiaceae

Grain diameter (equatorial axis 57.5 microns, polar axis 57.5 microns)

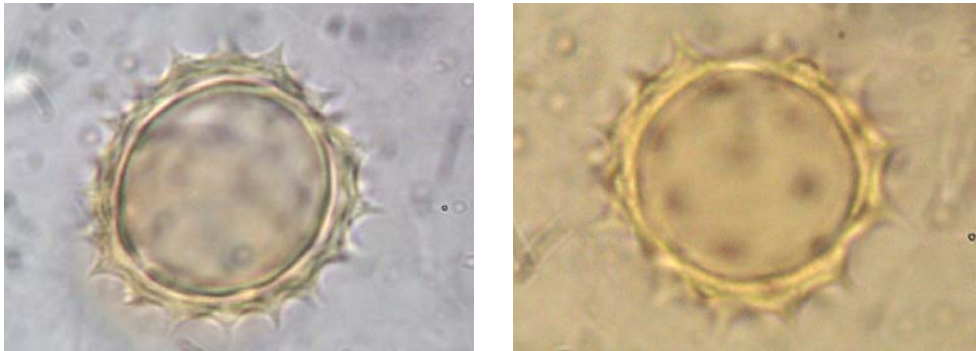
7) Family Caesalpiniaceae

Grain diameter (equatorial axis 42.5microns, polar axis 50 microns)

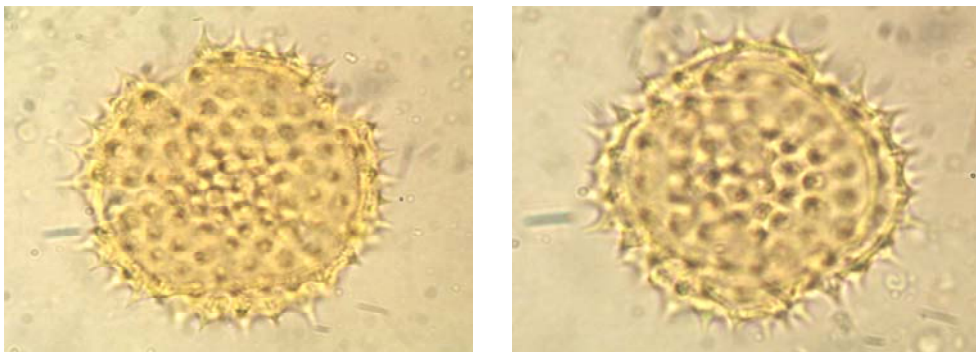
8) Family Mimosaceae

Grain diameter (equatorial axis 32 microns, polar axis 32 microns)

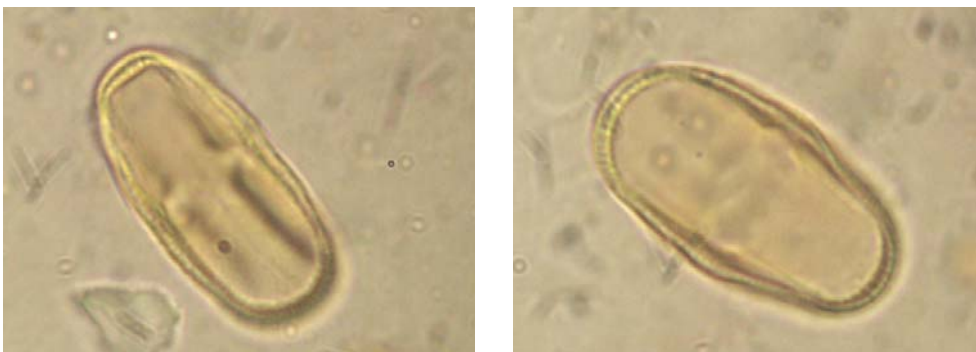
Figure 50 (Continued)

10) Family Astereaceae

Grain diameter (equatorial axis 20 microns, polar axis 20 microns)

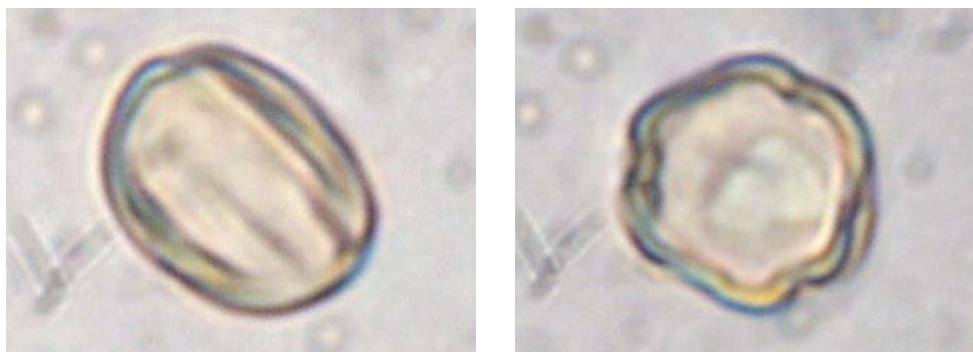
11) Family Asteraceae

Grain diameter (equatorial axis 34 microns, polar axis 34 microns)

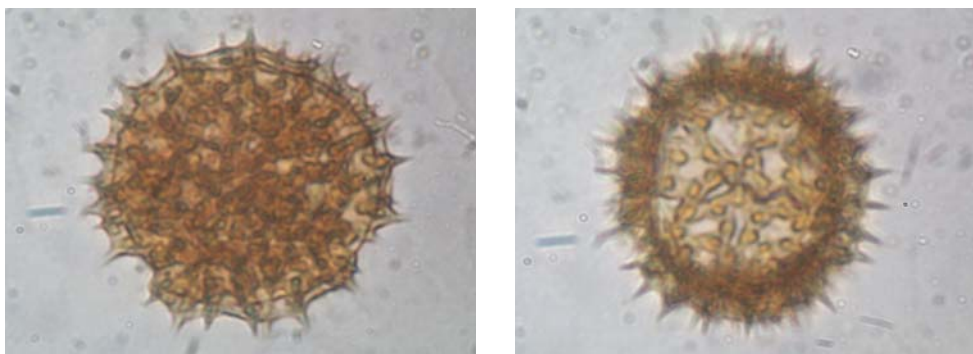
12) Unknown 36

Grain diameter (equatorial axis 15 microns, polar axis 27 microns)

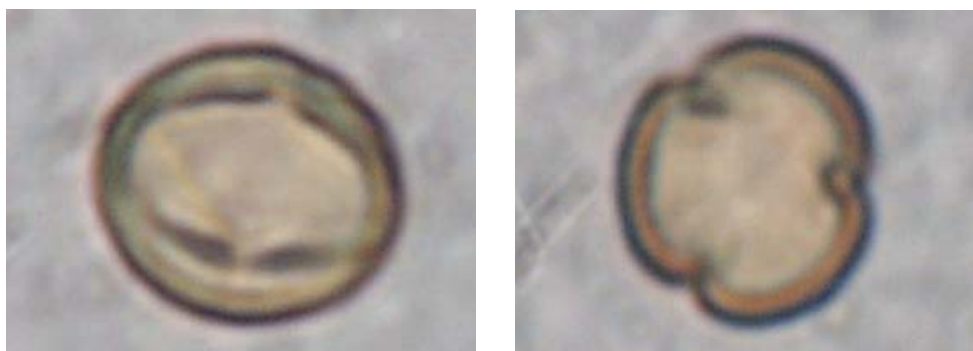
Figure 50 (Continued)

13) Unknown 37

Grain diameter (equatorial axis 25 microns, polar axis 22.5 microns)

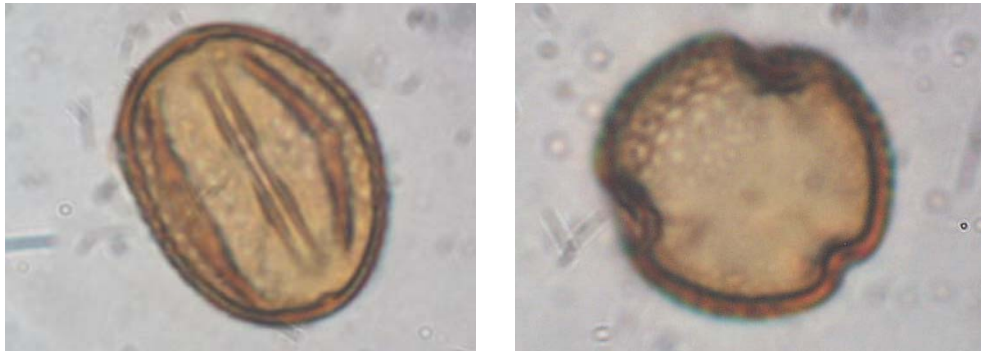
14) Unknown 38

Grain diameter (equatorial axis 43 microns, polar axis 43 microns)

15) Unknown 39

Grain diameter (equatorial axis 30 microns, polar axis 28 microns)

Figure 50 (Continued)

16) Unknown 40

Grain diameter (equatorial axis 38 microns, polar axis 32 microns)

Figure 50 (Continued)

DISCUSSION

1. Comparisons between stingless bee capturing methods

Previously, studies to compare the bee communities in different vegetation types or at different locations have used the number of nests per bee species per site (i.e. nest density) as the best estimate of bee abundance and species richness.

However, nest surveys gave limited data for assessing bee diversity due to the very high effort required to locate sufficient numbers of cryptic nests. Alternative methods were required. Potential alternative methods included either flower monitoring or honey-water baiting.

Flower monitoring has been successfully used to study bee communities in selected locations in the Neotropics (Heithaus, 1979; Wilms *et al.*, 1996). In a comparative study, Rincon *et al.* (1999) surveyed understory bees at flowers in logged and silviculturally treated rainforest plots in Costa Rica. Their results exhibited the problems inherent in the use of flower monitoring: numbers of species and numbers of individual bees strongly depended on the number of flowering plants present in plots at the time of the study. Due to the spatial and temporal variation of flowering, between-site assessments of bee diversity are bound to require large flower monitoring efforts over extensive periods of time. Additional problems arise because usually there is restricted access to the forest canopy where most flowering is likely to occur (Appanah, 1990; Momose *et al.*, 1998).

Preliminary trials at Thong Pha Phum investigated the use of a Malaise trap to survey for stingless bees. Malaise traps collect all insect that can fly. However, the trials at Thong Pha Phum, caught few insects and the majority of these were flies. This was probably because the siting of the trap was not optimal and because there was nothing to attract bees into the trap. Malaise traps work best when placed in sunny, semi-permanent insect flight paths (such as pathways in forests). It was not

possible to locate sufficient sites at Thong Pha Phum to both optimize catches of stingless bees and enable standardised comparison of forest types.

Eight water-based methods for capturing stingless bees were compared from January to March 2004 to optimize sampling methods. The diversity and mean numbers of stingless bees caught by all methods were recorded in four types of forest.

The bait trap method using a honey solution mixed with salt was more efficient at catching bees than any other methods. The most attractive bait was a 1: 1 mixture of honey and water, to which had been added a little household salt (NaCl). The salt provides some of the mineral requirements of the bees. Salt seeking is well known in tropical insects.

In nature bees often gather in groups to imbibe minerals from streams, pools or other water sources (Roubik, 2000). In some countries meliponine bees are known as “sweat bees” because of their habit of landing on humans to drink perspiration (which is salty). Tropical butterflies often form spectacular aggregations at pools or “salt licks”.

Pan trapping and the effect of pan trap color were also investigated.

For most insects, color is very important in flower detection and recognition (Keven *et al.*, 1996), and different colors attract different insects. There have been numerous studies on the color vision of honey bees (e.g. Giurfa *et al.*, 1995; Spaeth, 2001; Rodriguez-Girones & Santamaria, 2004). Bees have trichromatic vision based on ultraviolet, blue and green photoreceptors (Keven *et al.*, 1996). Giurfa *et al.* (1995) showed that *Apis mellifera* has color preferences for “bee-blue” (blue to human) and “bee-green” (yellow to human).

In the present study different methods of pan trapping (McEwen, 1997; Perry, 1997) were studied. At Thong Pha Phum stingless bees preferred yellow pan traps

more than other colors, which is consistent with the results of Yoke Mui (2005) who showed that *Trigona* spp. preferred yellow, artificial flowers to red and green flowers. Although red was visited least of all, there was no significant difference between red and green treatments, suggesting that bees have difficulties in separating red from green (Spaeth *et al.*, 2001).

At Thong Pha Phum, three different kinds of pan traps were set up (yellow, white and blue). Some bees were trapped after entering the trap or by the surface tension of the liquid. This method rendered the bees wet, making taxonomic identification difficult. Pan trapping had an additional, potentially serious disadvantage. The technique “works” because bees and other kinds of insects landing to visit the pan are trapped in the liquid and killed. The small quantity of detergent added to pan trap liquid breaks the surface tension and ensures that visiting insects break through the surface and drown. Thus, pan traps kill stingless bees indiscriminately and sometimes in large numbers, so there is a risk of the trapping techniques leading to large fluctuations in the the population of the bees.

As noted, the data from preliminary tests indicated that honey – bait (with salt) trapping was the best method for collecting bees in all forest types. This result agrees with Liow (2001) who used honey bait-traps to study bee diversity along a disturbance gradient in tropical lowland forests of peninsular Malaysia and Singapore. The present study at Thong Pha Phum is the first time that honey bait traps have been used to investigate the diversity of stingless bees in forest types in Thailand. The results revealed that there were differences among the diversity indices of stingless bees in the types of forest.

2. Taxonomic studies of stingless bees in Thong Pha Phum District, Kanchanaburi Province, Thailand

Taxonomic studies of stingless bees of South-east Asia has advanced due to a sound early foundation (Schwarz, 1937), subsequent excellent revisions (Sakagami, 1975, 1978), and the relatively small number of species. In Asia and the Sunda

Islands, there are three genera, *Trigona*, *Pariotrigona*, and *Lisotrigona*, with three subgenera, *Lepidotrigona*, *Homotrigona*, and *Heterotrigona* in the genus *Trigona* (Michener, 2000). There have been different systems for classifying stingless bees (Moure, 1961; Wille, 1979). Although these systems are still being modified, an interim system of special utility for studies in South-east Asia was presented by Sakagami (1982). In this system the subgenus *Heterotrigona* of Michener (2000) has been further divided into eight subgenera and five species groups.

Stingless bee samples from the study area were identified into morphological species by using the identification keys of Schwarz (1939) and Sakagami (1985). Identifications of all were species confirmed by Professor Charles Michener, of the University of Kansas, USA. Fourteen species, 7 subgenera and 3 genera were represented among the samples. Evidently, Thong Pha Phum District, Kanchanaburi Province represents a center of species richness for stingless bees. In this study area stingless bees exhibited the greatest abundance and species diversity so far recorded in Thailand (Saiboon, 1995; Michener and Boongird, 2002; Insoon and Savitree, 2006)

It is notable that one species of the genus *Lisotrigona*, *Lisotrigona cacciae* (Moure, 1961) was found in the study site. Species of *Lisotrigona* are uncommon members of the Indian and South-east Asian meliponinae fauna (Engel, 2000). Both Moure (1961) and Michener (1990) give useful accounts for the identification of *Lisotrigona*, while Michener (1990) provided a key to genera of the tribe Meliponini, which separates *Lisotrigona* from other stingless bee genera. *Lisotrigona* was known from only two nominal species: the type species, *Lisotrigona cacciae* (Nurse) and *L. scintillans* (Cockerell). Engel (2000) redescribed *L. cacciae*. *L. scintillans* (Cockerell) is now considered to be a junior synonym of *L. cacciae*.

L. pendleburyi which should be placed in the genus *Pariotrigona* (Michener, 2000). Saiboon (1996) found *Pariotrigona pendleburyi* (reported as *Hypotrigona pendleburyi*) in the south of Thailand and Insoon (2006); Pobsuk (2006) recorded the same species, also as *H. pendleburyi*, from Thong Pa Phum, Kanchanaburi Province.

In the course of this study one new species of *Trigona* has been discovered. This species belongs to the subgenus *Tetratrigona* and is distinct from but close to *T. sirindhornae*. The new species can be distinguished readily from *sirindhornae* by the color of the mesopleuron, which is uniformly black in the new species and predominantly reddish brown with a conspicuous, black, anteroventral mark in *sirindhornae*. *Trigona sirindhornae* was the first described from the south of Thailand but is now known to be more widespread geographically. The Thong Pha Phum collections lack eight of the 32 species recorded by Schwarz (1939) and 18 of the species currently recognised from Thailand (see Appendix B Table 1). Some absences can be explained. For example, some species, such as *T. fimbriata* seem to be most common in the north and northeast of Thailand (Boongird, 1998). *T. laeviceps* is more frequently found nesting in various artificial structures (such as house walls, pillars, palm fronds) in close contact with humans (Salmah *et al.*, 1990; Starr and Sakagami, 1987), i.e. situations which are relatively scarce in the forests of Thong Pha Phum. It is also possible that some stingless bee species remain to be discovered at Thong Pha Phum. To study the stingless bee fauna in the four types of forest represented at Thong Pha Phum this study used honey bait traps to attract workers and visual surveys of nests. It is possible that not all of the forest was covered by the surveys or that some species of stingless bee did not visit the honey bait traps.

The assemblages of stingless bees collected from honey bait traps are similar to the assemblages recorded in central Sumatra (Inoue *et al.*, 1990; Nagamitsu *et al.*, 1999b; Nagamitsu and Inoue, 2002).

The identification of meliponine bees can be difficult. In general, in this study it has been possible to distinguish species using morphological, color, behavioral and nest characteristics. However, the draft key shows how difficult it can be to express species differences unambiguously in a traditional, dichotomous key based on morphology and color. It may be possible in the future to overcome some of these difficulties by making use of digital tools, such as LUCID.

No attempt has been made so far to use molecular methods to study stingless bee taxonomy in Thailand. Our understanding of the stingless bee community at Thong Pha Phum Provides an ideal framework for future taxonomic work that might include molecular data.

3. Species richness and abundance of stingless bee

Data from honey–bait trap was used to investigate the stingless bees in four types of forest. The results revealed that there were differences in species richness and the abundances (number of individuals) among the types of forest.

Trigona ventralis and *T. sirindhornae* were the most abundant species in all forest types except DEF (Figure 26). *T. ventralis* was outstanding in DDF, where catches at honey baits were more than double the catches of the next most abundant species (*T. sirindhornae*). However, when data were disaggregated by season and forest types different species were found to dominate catches. Stingless bees were more abundant in the dry season than in the wet season. For most species, the number of workers collected at honey baits in the dry season was more than twice the number collected during the wet season. *P. pendleburyi* and *T. melina* were exceptional – catches of both of these species were greater during the wet season.

The results obtained from the present study show the variation in species richness and the abundances (number of individuals) between the four types of forest and between the sampling seasons. Stingless bees have their highest species richness in DDF (dry dipterocarp forest) and LMDF (lower mixed deciduous forest), which is relatively greater than species richness in UMDF (upper mixed deciduous forest) followed by that in DEF (dry evergreen forest). Stingless bees have their highest abundance in DDF followed by UMDF, LMDF and DEF.

Two different biodiversity analyses of honey bait data (Jaccard, Figure 29; Shannon Weiner, Figure 34) reveal the same clustering of forest types: the stingless bee communities in UMDF and LMDF are most similar to each other, DDF clusters

next to these two, and the stingless bee community of DEF is strongly dissimilar to the other three. UMDF and LMDF could be described as having “high or intermediate diversity, intermediate abundance” stingless bee communities, DDF as having a “high diversity, high abundance” stingless bee community, and DEF as having a “low diversity, low abundance” community.

Can these differences be explained by abiotic factors related to the structure of the forest types? Does DDF provides a more benign microclimate that is more suitable for successful foraging by stingless bees?

Several abiotic factors influence the activity of the bees and among them temperature has been mentioned as the most important. In addition the activity of some species is limited by the relative humidity (Corbet *et al.*, 1993). Temperature and Relative Humidity (RH) data certainly reveal that the forest types have somewhat different microclimates. A review of several authors (Iwama, 1977; Fowler, 1978; Kleinert-Giovannini, 1982; Guibu & Fonseca, 1984; Heard and Hendrikz, 1993) points out that in addition to food availability, flight activity of bees is influenced both by internal conditions of the colonies and by environmental factors. Temperature, relative humidity, light intensity, rainfall and wind speed all can influence the flight activity of stingless bees, although not always with the same intensity.

Light: Light levels are commonly expressed as “transmittance”. Growing-season transmittance is widely used in forestry because of its strong relationship to tree growth and survival. Results obtained from the present study were confirmed by Inson (2006) who studied transmittance by hemispherical canopy (fish-eye) photography. This technique was used to measure subcanopy light conditions in the four types of forest in Thong Pha Phum, Kanchanaburi Province. The results showed that the percentage of transmittances in wet season in LMDF was 7.73 followed by DDF, UMDF, DEF (6.60, 3.93 and 0.89% respectively). In the dry season the transmittance for LMDF was 15.88 followed by DDF, UMDF and DEF (12.35, 11.36 and 1.26% respectively). Thus, high light transmittance in DDF is associated with

high stingless bee species richness and abundance, and low light transmittance in DEF goes with low species richness and low abundance.

Temperature and Relative humidity: Temperature and radiation were the most important variables that affected insect flight activity at Thong Pha Phum. Temperature influences the intensity of activity above certain thresholds. Vapour pressure, cloud cover and wind speed had no significant effect on flight activity. Two variables correlated with flight activity in this study: temperature and Relative Humidity (R.H) data show that DEF, the forest type least favored by foraging stingless bees, had the lowest relative humidity and also had the highest air temperatures, in general, of all the forest types. On the other hand, CCA revealed that the group of species comprising *T. terminata*, *T. ventralis*, *L. cacciae* and *T. sirindhornae* (i.e. including the two most abundant species) increased in abundance with rising temperatures and decreased in abundance with rises in Relative Humidity (Figure 30). These results generally agree with those of Heard and Hendrikz (1993) who reported factors influencing flight activity of colonies of the stingless bee *Trigona carbonaria* in Australia. They considered temperature and light intensity as important factors that determine the flight activity of these bees. Colonies of *T. carbonaria* were active throughout the year at their experimental site, but the daily activity period was longer in the warmer months, and while the relative humidity did not show any significant effect. On the other hand Hilario *et al.* (2000) reported that flight occurred in *Melipona bicolor* mainly when the relative humidity was higher and temperatures were more moderate.

Thus, while abiotic factors (especially light transmittance, temperature and Relative Humidity) influence stingless bee abundance to some extent, they do not on their own explain the seasonal and forest-type differences in abundance recorded at Thong Pha Phum. These observations on flight activity lead to questions on the relationship between flight activity and body size.

Body size: Flight range: Roubik (1989) reported that stingless bees showed 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 flight range and the body size of the workers. The results of this study show that *T. ventralis* was most abundant, followed by *T. sirindhornae* both of which are medium-sized bees. These species have a greater flight range than small-sized bee (*L. cacciae*, *P. pendleburyi* and *T. fuscobatelta*). The results obtained agree with Kerr and Kerr (1999) who found that 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 *Torigona* (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. 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. On the other hand Kapyla (1974) remarked that the external activity depend on the body size of the insect, because larger species fly in lower temperature and intensities than smaller ones. The matter of flight range will be returned to in this Discussion after the following review of nesting and pollen foraging.

4. Similarity analyses of stingless bees in the four types of forest

Similarity analyses of stingless bees in the four types of forest (Figures 29 and 34) both indicated that the stingless bee fauna was the most similar in LMDF and UMDF, that LMDF and UMDF and DDF formed a cluster, and that the bee fauna observed in DEF was the least similar to those of the other three forest types.

1) Stingless bee species richness and abundance in dry evergreen forest (DEF) is clearly different from that in other forest types. Abiotic factors (temperature, relative humidity and light transmittance) were clearly different between DEF and other types of forest. In particular, DEF has much less moisture than other forest (52-90 R.H.%). This is significant because it is known that the activity of some species is limited by the relative humidity. For example, *Tetragonisca angustula* and *Plebeia emarina* do not leave their nests unless the relative humidity is higher than 70%

(Iwama, 1977; Kleinert-Giovannini, 1982). DEF also seemingly lacks tree species whose flowers are especially attractive to stingless bees (see Appendix B Table 13).

2) The species diversity and abundance of stingless bees in dry dipterocarp forest (DDF) is most similar to that in LMDF and UMDF. If we consider biotic factors (temperature, relative humidity, light transmittance) and the species of plants in the forest, there are no immediately obvious differences between DDF, UMDF and LMDF. However, the dominant plants in DDF do differ from those in mixed deciduous forests. Mixed deciduous forests have many Dipterocarpus trees, which produce gum and resin. Stingless bees collect these two products for the construction of their nests. The dominance of dipterocarps may account for the similarities between UMDF and LMDF stingless bee communities (Eltz, 2002). DDF has only four tree species whose flowers are especially attractive to stingless bees compared to eight or nine in UMDF/LMDF.

At Thong Pha Phum dry dipterocarp forests (DDF) are subject to annual fires during the dry season from December to May, with their peak in February-March. In certain, extremely dry sites, double burning in one season is common. These surface fires consume surface litter, other loose debris on the forest floor and small-sized vegetation. Fires also leave many trees with large, internal cavities, which are suitable for stingless bee nests. Thus, it may be that fire is an additional, important factor that sets DDF apart from LMDF and UMDF.

3) Finally, we can note that the similarities in species diversity and abundance between upper mixed deciduous forest (UMDF) and lower mixed deciduous forest and (LMDF) correspond to similarities in abiotic factors (temperature, relative humidity, light transmittance) and similarities in plant species. In these forest types dipterocarps provide nesting materials and there are eight in UMDF or nine in LMDF of tree species whose flowers are known to be attractive to stingless bees.

5. Nest surveys and nest aggregation

The present study provides the first detailed account of stingless bee nests, nest aggregations and nesting resources from natural forest areas in Thailand. It is based on a total of 103 nests belonging to 15 species of meliponines. The results are generally consistent with Eltz's (2001) account of stingless bee nests, nest aggregations and nesting resources from natural forest areas in Malaysia. That account was based on a total of 275 nests belonging to 12 species of meliponines.

Sakagami *et al.* (1990) list 28 species of Meliponini from the whole of Borneo, and data from honey-baiting suggests that up to 22 species can occur sympatrically in a Bornean lowland rain forest locality (Roubik, 1996). Thus, in this study nest surveys located about one half of the regional stingless bee assemblage.

Several studies have found that Asian stingless bee nests commonly aggregate in individual nest trees (Roubik, 1996; Nagamitsu and Inoue, 1997; Eltz *et al.*, 2003). In the present study up to 27 nests were situated in a given tree, and aggregations consisted of up to 8 different species of bees. In contrast, in Sabah, Eltz (2001) recorded a maximum of only three species per tree and the greatest nest count was a modest eight nests per tree.

Among the species whose nests were not located by our surveys, at least 9 are known to be cavity-nesting species whose nests have been recorded by previous authors from Thailand (Klakasikorn *et al.*, 2005). Lack of canopy access and difficulties of detecting canopy colonies may have particularly biased our data for species nesting in small cavities in major branches of canopy trees. Some species (*T. laeviceps*) are more frequently found nesting in various artificial structures (house walls, pillars, and palm fronds) in close contact with humans (Salmah *et al.*, 1990; Starr and Sakagami, 1987; Roubik, 2000).

Generally, stingless bee nests were heavily aggregated within individual nest trees in Bornean forests. Although this trend was apparent in all species that were

found in large numbers, aggregated nesting was particularly pronounced in *T. collina*, (favoring conspecific aggregations) and in *P. pendleburyi* (showing a tendency to form mixed aggregations with any of the other base-nesting species). At Thong Pha Phum, *T. collina* nests were the most commonly encountered nests (20.39% of all nests) and they were highly aggregated (92.3% of nests). Only one *P. pendleburyi* nest was discovered, in association with *T. ventralis*. In Sabah Eltz (2001) found that the majority of his aggregated *T. collina* nested with conspecifics rather than with other species as at Thong Pha Phum. In Sabah *P. pendleburyi* seemed to prefer to nest in mixed aggregations. *P. pendleburyi* was discovered only once at Thong Pha Phum, in association with *T. ventralis*.

Clustering of nests in trees has been reported by several authors (Starr and Sakagami, 1987; Salmah *et al.*, 1990; Roubik, 1996), but the reasons for aggregating are poorly understood. Limited availability of suitable nest sites may be one possible cause, especially in degraded areas that lack sufficient numbers of natural tree cavities.

In the four types of forests studied at Thong Pha Phum, nest cavities are more likely to be limited. Aggregation is certainly very common with 92.3% of *T. collina* nests in aggregation, 93.75% of *T. ventralis* nests, 91.67% of *T. sirindhornae* nests and 100% of *T. terminata* nests. One tree (*Ficus* sp.) hosted 26 nests and 7 bee species.

Here, clustering also may be favored by mechanisms related to how new nest sites are located by bees. In stingless bees colony multiplication is started by scout bees that search for suitable nest sites (Michener, 1974; Inoue *et al.*, 1984b).

Eltz (2001) has suggested that the scout bees of at least some species may be attracted to volatile chemicals given off by existing nests, and are more likely to establish new nests in association with other stingless bees. It is possible that some nests are founded by scouts which fly only a short distance from the maternal nest and return, or scouts which search widely but unsuccessfully for a new site. (see also

Hubbell and Johnson, 1977, for *T. fulviventris* in Costa Rica). This would account for a number of conspecific aggregations. Aggregations may be able to defend the nest tree more effectively.

It could be simply that the number of suitable nesting sites is limited, so that available sites are exploited to the fullest extent. The large number of mixed aggregations at Thong Pha Phum would support this.

Eltz (2001) remarked on the apparent lack of inter- and intra-specific aggression among stingless bees at his Sabah sites. At Thong Pha Phum District, Kanchanaburi Province, I observed many thousands of stingless bee workers and rarely observed signs of aggression between individuals.

It is intriguing to note that the aggregations of stingless bee nests observed in South-east Asia (Starr and Sakagami, 1987; Salmah *et al.*, 1990; Eltz, 2001; this study) are not so common elsewhere. Aggregations appear to be much less common in New World stingless bees. There stingless bees are more dispersed and it has been suggested (e.g. Hubbell and Johnson, 1977) that competition for resources and aggression between bees from different colonies is the cause of this. In the open woodlands of northern and north-eastern Australia, where floral resources are often scarce for long periods, stingless bees also appear to be more dispersed. Neither Rayment (1935), Michener (1961) nor Dollin *et al.* (1997) refer to the phenomenon of nest aggregation. Little has been published on the stingless bees of the Australian rainforests, where certainly there are plenty of *Ficus* capable of sustaining multiple nests.

6. Nest Density

This is the first study of stingless bee nest density in Thailand. Nest density of stingless bees in Thong Pha Phum District, Kanchanaburi Province, varied 20-fold between sites in this study, ranging from a mean of 0.66 nest/ha in DEF to a phenomenal 15.66 nests/ha in LMDF. The result was consistent with Eltz (2000) who

reported nest densities of stingless bees in dipterocarp forests in Sabah varied more than 20-fold between sites, ranging from a mean of 0.5 to 0.7 nest/ha in Deramakot and Danum Valley to a remarkable 16.2 nests/ha in mangrove-bordering forests in Sepilok.

Differences in nest density between the forest types may reflect the influence of forest structure, food resources or microclimate, all of which vary among the forest types.

Appendix C Figure 1 reveals that the forest types have somewhat different microclimates. Significantly, DEF, the forest type least favored by stingless bees as a nesting site, tends to be drier than the other forest types. If the relative humidity in each month is compared across the forest types, it can be seen that DEF had the lowest or equal lowest relative humidity during 8 of the 12 months between April 2004 and March 2005. DEF was also hotter, in general, than the other forest types. In 8 of the 12 months, DEF had the highest or equal highest air temperature.

In contrast, LMDF, the forest type favored by stingless bees as a nesting site, was the driest of the forest types during only one month (June 2004) and was hottest or equal hottest during only two months (June 2004 and March 2005).

These observations suggest that LMDF provides a more benign microclimate. This may be more suitable for successful nesting by stingless bees.

It is interesting to compare the data from honey-bait traps and nest density. Some data sets correlate reasonably well. For example, *T. collina* nests in UMDF and LMDF where the highest honey bait catches for this species were obtained. Moreover, it is absent from DDF and DEF where honey bait catches for this species were low. Similarly, *T. ventralis* nests were present in DDF, UMDF and LMDF, where high honey bait catches for this species were obtained. No *T. ventralis* nests were discovered in DEF and honey bait catches for *T. ventralis* in this forest types were zero.

However, other data sets do not correlate at all. For example, *T. terminata* was found nesting in UMDF and LMDF and was not discovered in DDF or DEF. However, the highest honey bait catches for this species were in DDF—indeed much larger numbers of bees were taken than at honey baits in either UMDF or LMDF. Equally perplexing is the observation that the scarce species, *T. thoracica*, nests only in LMDF but was taken in ample numbers at honey bait traps in both LMDF and DEF.

It is possible that some nests were overlooked during the nest density survey. Lack of canopy access and difficulties of detecting canopy colonies may have particularly biased our data for species nesting in small cavities in major branches of canopy trees.

Alternatively, apparent inconsistencies between honey baiting and nest data could be explained by assuming that stingless bees forage into forest types different to the forest types in which they have established nests.

Nest density generally declined over the three years of the study. This was a result of progressive and distinct reductions in the numbers of nests of the most commonly encountered species.

7. Nest trees

At Thong Pha Phum stingless bee nests occurred in or at the base of a variety of different tree species (Appendix B Table 9). Eltz (2001) made similar observations in Sabah. His data demonstrated a proportional increase of nest tree diversity/bee species with nest tree sample size. A similar relationship appears to exist for meliponines in Costa Rican dry-forest (Hubbell and Johnson, 1977). The three studies together suggest that stingless bees are opportunistic in their selection of nest sites. It seems that they are not especially selective of tree species and are likely to colonize any tree offering a suitable cavity of the right size. Of course, some tree species naturally tend to form suitable cavities because of characteristics of their wood or

their growth characteristics. Most nest trees had a diameter of about 150 cm (dbh). Some trees which had a diameter of more than 250 cm had 6-8 bee nests. Tree species that are especially suitable for bee nests are those that tend to form hollows accessible to bees through crevices between the living and dead parts of the trunk (Eltz, 2001).

8. Nest entrances

The kinds of entrances seen in this study have all been recorded elsewhere previously and appear to be typical of the various species. The nest entrances of two species of stingless bee, *T. melina* and *T. atripes*, are described here in detail for the first time.

The function of these diverse and elaborate entrances is possibly three-fold in that they assist (1) the orientation of returning bees, (2) the defense of the nest, and (3) general nest cleanliness.

1) Presumably the inter-specific differences and the prominence of the entrance structures help workers locate and return to their correct nest. This may be of particular importance where multiple species nest in close proximity.

(2, 3) Generally, stingless bees are believed to be relatively immune to ant predation due to their use of sticky resins for colony defense (Salmah *et al.*, 1990). The elaborate nest entrances (such as those of *T. apicalis*, *T. melanoleuca*, *T. melina*, *T. pagdeni* and *T. fuscobalteata*) may also assist in excluding accidental intrusion by dirt, plant material, or insects or spiders walking over the substrate. The entrances provide narrow points of access that can be blocked by massed bees in the case of threat by predators or parasites. This is especially important because these bees cannot call upon a venomous sting to protect their provisions, brood and queen. This interpretation is consistent with the report of Roubik (2006) that the primary activity of non-foraging bees near their nest entrances is the physical prevention of entry by small insects, including parasites and the deposition of fresh resin on the external

entrance tube, which may deter ants. This reasoning also agrees with Melo (1996) that individual variation in architecture, for instance in the elaboration of the nest entrance or the thickness of resin enclosing the internal nest, likely relates to nest age, bee genetics and/or aspects of the micro-environment, including predators, parasites, rain, wind (humidity, temperature) and sun (light or direction). The chemistry and choice of nest resins as repellents of natural enemies has not been studied, although the antibacterial properties of resins are well known (Langenheim, 2003.; Inson6).

Intraspecific variation between nest entrances can sometimes be explained by local characteristics of the substrate. At Thong Pha Phum nests of *T. apicalis*, *T. terminata*, *T. ventralis* and *T. sirindhornae* sometimes varied in color, probably because the gum that was used by the worker bees to construct the entrance had been harvested from different species of trees. Roubik (2006) noted that currently there is little understanding of how variation in micro-architecture may be adaptive. On some occasions, a nest construction techniques can be related to specific constraints. For example, *Melipona* forage for small pebbles and stones and then employ them in their nest construction. Building material of this mass could not even be lifted by most stingless bees.

The simplest stingless bee nest entrance protrudes slightly from the base of the entrance hole. *Trigona collina*, *T. artipes* and related species build a very long but slender nest entrance tube. The tube becomes more and more elongate by the progressive placing of fresh resin on the end of the tube. The largest bees in Southeast Asia, *Trigona thoracica* have an enormous, projecting nest entrance. The entrances are so large that their weight makes them periodically fall from the host tree. These large bees have no accessory galleries or lamellate passageways at the entrance, and no aggressive nest defense behavior. Stingless bees that have exposed nests tend to have aggressive defensive behavior. Stingless bees that appear well protected, settled within several centimeters of living tree trunk and having a small nest entrance, can be either aggressive or timid. (such as *L. cacciae* and

P. pendleburyi). The narrow tube can be closed with resin or cerumen, or coated outside with droplets of fresh resin where invaders like ants may be halted. In contrast at Thong Pha Phum the aggressive stingless bee (*T. canifrons*) has a relatively small, simple entrance. This is consistent with the report of Sakagami (1983) that the aggressive stingless bee, *H. itama* that was aggressive stingless bee had a small and simple entrance.

9. Daily Foraging behavior of stingless bees

In general, the data reveal a fairly consistent daily pattern of foraging. The numbers of foragers tend to increase from about 9.00 a.m. to about 11.00 a.m., reach their maximum levels from about 12.00 noon to 2.00 p.m, and decline throughout the afternoon (e.g. Figure 37). Occasional surges in activity sometimes disturb this rhythm (e.g. *T. collina* mid morning, *T. apicalis* in the late afternoon) but in general the pattern is consistent across the seasons, bee species and forest types. Individual species have more or less similar patterns across the forest types. A few species exhibit individual characteristics. For example, by 9.00 a.m. the large species, *T. apicalis* tends to have reached near-maximum forager numbers. In contrast, the smaller *T. ventralis* and *T. sirindhornae* are “late starters” and their forager numbers increase noticeably throughout the morning.

10. Seasonal Pollen foraging behavior of all stingless bees from four types of forest

In general, the percentage of stingless bee workers foraging successfully for pollen was low during the wet season and increased steadily with the onset of the dry season (e.g. Figure 41). Similarly, as revealed by honey baiting in all forest types, stingless bee abundance generally was low during wet season months and high during the dry season (Figure 42). An exception to this were the spikes in abundance of *T. ventralis* in DDF during several wet season months – see Figure 41).

T. apicalis can be compared across the forest types and exhibited broadly similar patterns across each forest type. Fluctuations in pollen foraging percentages were greatest in DDF. Pollen forager percentages tended to be higher in DEF and DDF., suggesting that *T. apicalis* nesting in DEF and DDF have access to resources that are highly suitable to this species.

Where several species could be compared (UMDF, LMDF) *T. apicalis* emerged as the most successful forager. It recorded the highest percentage of successful foragers in 6 of the 12 months in UMDF and in 8 of the 12 months in LMDF. However, bee size cannot be the only factor determining this, since the large bee species *T. melanoleuca* and *T. canifrons* were not nearly so successful.

The small *T. ventralis* had the unenviable distinction of having the poorest pollen-foraging percentages in 9 of the 12 months. Again, however, size cannot be the only factor involved, since the small *T. sirindhornae* never had the lowest percentage of pollen foragers.

It is interesting to compare the pollen percentage data for UMDF and LMDF. *T. apicalis* and *T. ventralis* are present in both (as well as several other species). In both forest types *T. apicalis* nests had the overall most successful foragers (6 of 12 months in UMDF, 9 of 12 months in LMDF) and in both forest types *T. ventralis* nests had the overall least successful foragers (5 of 12 months in UMDF, 9 of 12 months in LMDF). LMDF appears to be the most challenging / competitive habitat – in 9 of the 12 sampling months the lowest percentage of successful foragers (taking into account all species) was recorded here.

It is useful to compare the successful forager percentages with the flowering phenology data of Appendix B Table 10 – 13. In DDF there is broad correlation between forager percentages and number of plant species in flower. The low percentages in June – September correspond to a period of especially low flowering: only *Gardenia sootepensis* in June - July and only *Dillenia indica* in August - September. However, forager percentages improved markedly in October when there

was no flowering and reached a maximum in November when only *Crypteronia paniculata* and *Dipterocarpus obtusifolius* were flowering.

In UMDF there was also broad correlation between forager percentages and the number of plant species in flower. Especially low pollen foraging percentages in May – September corresponded to a period when there was 10 or fewer plant species in flower, compared to 13-24 species in January-April. There was a steady increase in pollen forager percentages from October to January, corresponding to a steady increase in the number of plant species flowering (October, 1 species; November, 4 species, December, 6 species and January, 17 species, respectively). The highest pollen-foraging percentage was in February which was the month with the most plant species in flower (24). The decline in pollen-forager percentages in March was more abrupt than the decrease in the number of plants species in flower (24 to 22).

In LMDF there was broad correlation between forager percentages and number of plant species in flower. During May-September there were steady increases in pollen-foraging percentages and in October-January The pollen forager percentage. in February, which is the month in which most plant species were in flower, was high (29). However, the increase in pollen forager percentages October-December was more marked than the increase in the number of plant species coming into flower (October, 1 species; November, 0 species; and December, 4 species, respectively). As in other forest types there is a rather abrupt decline in pollen forager percentages in March, although the number of plant species in flower remained high (down to 27 from peak of 29 in February).

In DEF there was broad correlation between forager percentages and the number of plant species in flower. Low forager percentages in July-September corresponded to a period of minimum flowering (plant species flowering July, 2 species; August, 2 species and September 1 species, respectively). The high pollen foraging percentage in February corresponded to peak flowering (12 plant species). As in other forest types there was a rather abrupt decline in pollen foraging

percentages in March, although the number of plant species in flower remained high (down to 10 from 12 in February).

In DDF there was a long period (June-November) when no more than one plant species was flowering. This should make DDF a difficult habitat for stingless bees. However, honey bait data demonstrates that species richness was high in DDF (and in LMDF) and that bee abundance was greatest in DDF, in both wet and dry seasons. Even though there was a long period with seemingly few floral resources between June and October, stingless bees were able to survive quite well in DDF.

In summary, the number of plants flowering in the dry season is much greater than the number of plants flowering in the wet season. This broadly correlates with pollen foraging percentages, i.e. larger percentages of successful foragers in the period October – March than in the period May-September. The number of plant species in flower steadily increases from October to December, correlating broadly with increasing pollen forager percentages. The maximum forager success in February corresponds to the peak of flowering (March in DDF; February in LMDF, UMDF and DEF). However, the decline in pollen forager percentages in March 2005 was rather abrupt while the decline in the number of plant species in flower was more gradual.

11. Number of types of host plants

The data reveal an annual pattern in pollen collecting that is generally consistent for all stingless bee species in each forest type (Figure 44). In general, at Thong Pha Phum stingless bees collect a low diversity of pollen types in the early to mid wet season. This diversity begins to increase in the late wet season. The highest diversity of pollen types is utilized in the dry season and especially during the December-January period. At the low point of pollen diversity in the early wet season, stingless bee workers at Thong Pha Phum were commonly collecting only 2 to 4 types of pollen. However, during the December-January period *T. apicalis* was utilizing

between 9 and 11 different types of pollen, depending on month and forest types and *T. canifrons* foragers were bringing up to 12 different pollen types to their nests.

Trigona ventralis exhibited an anomalous pattern in UMDF. Figure 44 shows that in the early wet season (October 2004) *T. ventralis* foragers were collecting a greater variety of pollen types (7) than the other three species (*T. apicalis* 6 types, *T. collina* 5, *T. terminata* 3) but in subsequent months collected a decreasing variety of pollen, while the other three species followed the general pattern and collected an increasing diversity of pollen. Figure 41 reveals that during this period the percentage of pollen foragers for all four species in UMDF was roughly the same and trending upwards. It appears that from November to February in UMDF, *T. ventralis* workers were foraging as successfully as the workers of other three species but were doing so by concentrating on a smaller number of plant species.

It is interesting to compare the flowering data of Appendix B Table 11-13 (obtained by direct observation) with the number of pollen types collected by bee species.

In DDF (Figure 46) the variety of pollen types collected by stingless bees (*T. apicalis*) exceeded the number of plants observed to be flowering in 7 of the 12 months, most notably in months of low flowering frequency. In UMDF, LMDF and DEF the number of pollen types collected exceeded the number of plants observed flowering in 6, 4 and 7 months respectively. Could the direct observational data underestimate flowering and that when flowering is at relatively low levels, stingless bees are better at finding scarce flowers than humans or is something else happening?

Let us consider first the data for the late wet and early dry season. In DDF, *T. apicalis* workers were able to find between 4 and 6 different pollen types during the late wet season – early dry season months between August and November, a period during which only 1 or 2 species of plants were observed to be in flower. By January

2005, *T. apicalis* workers were utilizing their maximum diversity of pollen types (9 types) at a time when 10 plant species were in flower.

In UMDF, between August and September, the four species (*T. apicalis*, *T. collina*, *T. terminata* and *T. ventralis*) were utilising between 2 and 8 pollen types, at time when only 2-4 plant species were observed in flower. In December-January the four species were utilising between 6 and 9 pollen types (*T. apicalis*, *T. collina*, *T. terminata*) or 3-4 types (*T. ventralis*) at a time when between 6 and 17 plant species were observed flowering.

In LMDF, between August and September, the six species (*T. apicalis*, *T. melanoleuca*, *T. canifrons*, *T. collina*, *T. ventralis* and *T. sirindhornae*) were utilising between 3 and 12 pollen types, at time when only 0 – 4 plant species were observed in flower during any one month. In December – January the six species were utilising between 9 and 13 pollen types at time when 4 - 18 plant species were observed flowering

In DEF, *T. apicalis* workers used between 3 and 9 different pollen types between August and November, a period during which only 2-3 species of plants were observed to be in flower. By February 2005, *T. apicalis* were utilising their maximum diversity of pollen types (9 types) at a time when 12 plant species were observed in flower.

Let us consider now the data for the late dry season. It is noticeable that the diversity of pollent types utilised by the stingless bees fell sharply in the late dry season months of February and March. This occurred even though direct observation indicated that these months were the period of maximum flowering diversity. In DDF 14 and 26 plant species were flowering in February and March respectively, but the number of pollen types utilised by *T. apicalis* fell from 8 (February) to 3 (March).

In UMDF 17, 24 and 22 plants were in flower in January, February and March respectively but the number of pollen types utilised by *T. apicalis* fell from 9 to 6 to 4, the number utilised by *T. collina* fell from 8 to 7 to 2, and the number utilised by *T. terminata* went from 6 to 4 to 5. As noted above, *T. ventralis* was anomalous and the number of pollen types collected by its workers was 3, 3 and 4 respectively.

In LMDF 29 and 27 plants were observed flowering in February and March respectively. The number of pollen types utilised by the six species monitored all fell: from 11 to 5 for *T. apicalis*, from 8 to 6 for *T. melanoleuca*, from 9 to 4 for *T. canifrons*, from 12 to 7 for *T. collina*, from 11 to 7 for *T. ventralis* and from 12 to 3 for *T. sirindhornae*.

In DEF 12 and 10 species of plants were observed flowering February and March respectively. *T. apicalis* utilised between 7 and 11 pollen types in February and only 4 – 5 in March.

Figure 41 reveal that from February to March the percentage of pollen foragers declined sharply for all species in all forest types. Thus, although floral diversity was apparently at its greatest, pollen foraging was declining across all of the stingless bee communities at Thong Pha Phum. Honey bait data reveals that stingless bee population levels in March are relatively high: in DDF, UMDF and DDF the populations were at their second highest levels, and in LMDF at their third highest. Data to hand at present do not offer a ready explanation for this sharp decline in pollen foraging.

Stingless bee pollen food sources were identified into 112 plant species belonging to 38 families. The diversity of pollen collected by stingless bees in Thong Pha Phum is higher than that observed previously in any other forest. Jongjitvimol *et al.* (2006) recorded the pollen collected by three species of *Trigona* (*T. apicalis*, *T. collina* and *T. fimbriata*) at the Phitsanulok Wildlife Conservation Development and Extension Station in Northern Thailand. There, these three species foraged on a total of 29 plant species representing 18 families: Acanthaceae, Agavaceae,

Alangiaceae, Arecaceae, Asteraceae, Bignoniaceae, Caesalpiniaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Lythraceae, Mimosaceae, Papilionaceae, Rubiaceae, Scrophulariaceae, Thunbergiaceae, Verbenaceae and Zingiberaceae. Dejtisakdi *et al.*, (2005) surveyed stingless bee species and melliferous plants in deciduous forest in Chiangmai Province (which is also in northern Thailand) and found that *T. collina* and *T. ventralis* visited 19 and 15 plant species respectively. Kaekaw (2007) also studied stingless bees in Chiangmai Province but in lower mountane evergreen forest where *T. ventralis* visited some 50 plant species from the families Euphorbiaceae, Fagaceae and Rubiaceae.

12. Foraging behavior, forest types and foraging capabilities

Pollen foraging data reviewed in the previous section here can be explained, at least in part, by.

- 1) The type of forest and the proximity of that forest to other pollen resources.
- 2) The foraging behavior and capabilities of the different species of stingless bees.

1) Type of forest

It is particularly noticeable that in DDF there was a long period from June to November when no more than one plant species was flowering. Also, Appendix B Table 13 reveals that only four tree species whose flowers are especially attractive to stingless bees occur in DEF. These two observations would suggest that DDF is a difficult habitat for stingless bees. However, honey bait data demonstrated that stingless bee species richness is high in DDF and stingless bee abundance is greatest among the forest types in DDF in both wet and dry seasons. Stingless bee nests are moderately numerous in DDF. How are we to explain this apparent anomaly? The key observation is that the pollen types collected by *T. apicalis* are almost completely absent from plants in DDF. At Thong Pha Phum DDF is located on the top of a mountain. The area occupied by DDF is very small, very long and narrow. Winds

tend to be very strong and stingless bees cannot collect pollen from tall plants in windy conditions. However, right beside DDF at Thong Pha Phum is a tract of upper mixed deciduous forest. It is possible that stingless bees that nest in DDF fly outside DDF to collect pollen from plants in UMDF.

In UMDF the pollen collected by the four stingless bee species nesting in UMDF is quite similar. This is probably a result of all of the bee nests studied being located in the same tree. Each bee species would have had ready access to the same flowering plants. UMDF contains eight tree species whose flowers are attractive to stingless bees.

In LMDF the results show that the number of types of pollen collected by stingless bees that nest in LMDF is higher than that in any other forest type. This is consistent with honey bait data indicating high species richness in LMDF and with the high nest counts in this type of forest. All of this may be in large part due to the proximity of this forest type at Thong Pha Phum to gardens, orchards and human habitation. LMDF also contains nine tree species whose flowers are attractive to stingless bees. Almost certainly stingless bees can fly from their nests in LMDF and collect many types of pollen outside the forest. On the other hand UMDF, DDF and DEF at Thong Pha Phum are far from gardens and orchards and the stingless bees nesting in these forest types can collect only few types of pollen.

In DEF the pollen types collected by *T. apicalis* were almost completely absent from plants in DEF. DEF contains no trees whose flowers are particularly attractive to stingless bees. Honey bait data reveal that stingless bees have low species richness and abundance in DEF. Nest counts are also low. At Thong Pha Phum DEF occupies a small area adjacent to lower mixed deciduous forest. It is possible that stingless bees nesting in DEF fly from DEF to collect pollen from plants in LMDF. However, even with access to this potentially richer resource, DEF supports a modest stingless bee community.

Data presented here suggest that stingless bee population densities in forests are chiefly determined by the local availability of food resources. Stingless bees were particularly abundant in forest fragments where bees had access to floral resources in adjacent, non-forest habitats.

In fact, data from LMDF suggest that non-forest plants can provide huge rewards to individual foragers and superior resources for their colonies, thereby increasing the stingless bee carrying capacity of edge forests. For example Longan (*Dimocarpus longan* Lour.), which heavily dominated bee diets in LMDF edge forest, is the most abundant tree of the area. The same is true for teak (*Tectona grandis*), pollen of which was collected in quantities by stingless bees in a site bordering a plantation. Data on flowering phenology in plantations and on roadsides are lacking from this study.

Evidence from other studies supports the idea that alternative food sources mediate increased bee nest densities. It has been suggested that floral resources provided by farmland increase stingless bee abundance due to their being available during times when natural habitats become dry and unproductive.

The results from this study at Thong Pha Phum emphasise that the positive effect of crop plants on stingless bee populations will depend heavily on the kind of crop or plantation. Diverse agricultural landscapes like those bordering LMDF at Thong Pha Phum are likely more beneficial to stingless bees than are monocultures or natural forest (UMDF, DDF and DEF). The conclusion is supported by Fye (1972) who noticed that the activity of nesting bees was more pronounced in disturbed and open areas than in continuous forest. Gathmann *et al.* (1994) also reported that diverse vegetation obviously supplies a greater amount of nutritious pollen and thereby supports more bee species. “Non-natural” plantings can assume great importance for bee populations. For example, Corbet (2000) studied populations of bumble bees and observed that in some situations, crop plants with extended flowering seasons may even represent a keystone resource for certain bumble bee species.

Of course, another important determinant of a potential pollinator's choice of plants lies in the ability of a flower to attract bees using color, size, odor, time of opening, etc. The height and position of a flower on a plant are also of importance to visitors (Ramirez W., pers. com.). This leads us finally to consider the behavior of different species of stingless bees and their differing capabilities.

2) The foraging behavior and capabilities of stingless bee

T. apicalis is a large size of stingless bee and data presented here confirm that workers of this species can collect many different types of pollen. The results are supported by Roubik (1989) who reported that large stingless bees can forage over 1 km from their nests. There are some correlations between flight range and the body size of the workers, indicating that smaller species are restricted to smaller flight ranges and thus are able to forage over smaller areas overall. Kerr and Kerr (1999) also found that large bees have greater flight ranges than small bees. However, large size does not convey overwhelming advantages. Large bees may have difficulty in prying open small, tightly closed floral parts when the flowers are still on the tree, or may find it difficult to reach tall plants (W. Ramirez, pers. com.). Furthermore, some types of pollen are dry, and non-sticky at anthesis to facilitate wind dispersal. This probably makes it difficult for stingless bees to accumulate pollen loads. After the flowers fall to the humid ground the grains become stickier (Miranda, pers. com.) so they can be gathered into pollen loads and carried. Thus, stingless bees with a disposition to forage low to the ground could make use of this kind of pollen resource.

There is evidence that different species of stingless bees have different foraging preferences or make different floral choices (e.g. stratum preference, color preference, etc.) rather than taste.

In summary, stingless bee species differ in their capacity to fly to and utilise floral resources. Small species may be restricted to resources near to their nests. Larger species may be able to fly longer distances from habitats that provide nest sites.

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

From the experimental results and discussion of this study, conclusions can be drawn as follows:

- 1) The stingless bee fauna of western Thailand is highly diverse at the generic and species level.
- 2) Species richness and abundance of stingless bees varied with the season and bees were most abundant during the cooler, drier months of the year. Species abundance was directly affected by the fluctuation of individual species populations. Several factors influenced the activity of the bees, in particular temperature, relative humidity, light transmittance, body size and flight range.
- 3) Nest density generally declined over the three years of the study. This was a result of progressive and distinct reductions in the numbers of nests of the most commonly encountered species. The results were influenced by the temperature and Relative Humidity, revealing that the forest types have somewhat different microclimates.
- 4) The kinds of entrances seen in this study have all been recorded elsewhere previously and appear to be typical of the various species. The nest entrances of two species of stingless bee, *T. melina* and *T. artipes*, are described here in detail for the first time. The function of these diverse and elaborate entrances is possibly in that they assist (1) the orientation of returning bees, help workers locate and return to their correct nest. (2) the defense of the nest, stingless bees are believed to be relatively immune to ant predation due to their use of sticky resins for colony defense (3) general nest cleanliness.

5) In general, at Thong Pha Phum stingless bees collect a low diversity of pollen types in the early to mid wet season. This diversity begins to increase in the late wet season. The highest diversity of pollen types is utilized in the dry season. At the low point of pollen diversity in the early wet season, stingless bee foragers at Thong Pha Phum were commonly collecting only 2 to 4 types of pollen. Floral resources outside the forest type in which the bees nested can be critical to the prosperity of stingless bees.

6) The daily foraging behavior was fairly consistent for all species of stingless bees at Thong Pha Phum. The numbers of foragers tended to increase from about 9.00 a.m. to about 11.00 a.m., reach maximum levels from about 12.00 noon to 2.00 p.m, and decline throughout the afternoon.

7) Nest aggregation is common at Thong Pha Phum, in part because high quality nesting sites are available in limited numbers, and possibly because of natural tendencies among stingless bees to establish new nests near to existing stingless bee nests.

8) The differences between the forest types and their stingless bee communities have been summarised in the following table. For example, LMDF is revealed as a particularly favourable place for stingless bees and DEF as particularly challenging. The Figure 30 also illustrates that the diversity and abundance of stingless bees are influenced by a number of inter-related factors, touched upon in this study. Nest density is influenced by the availability of hollow trees suitable for nesting, which in turn depends on the floristic composition of the habitat and the fire history. Abiotic factors such as temperature, relative humidity and light levels influence both nesting and flight preferences of stingless bees. The availability of nesting materials, especially resin and gum, is also of importance. Of course, the availability of floral resources is a hugely determining factor. Some forest types clearly offer a greater range of flowers that are attractive to stingless bees. However, it is clear that floral resources beyond the nesting place can exert strong influences over stingless bee communities.

	DDF	UMDF	LMDF	DEF
Species richness	High (9 species)	Intermediate (7 species)	High (9 species)	Low (5 species)
Species abundance	High (7,428)	Intermediate (4,079)	Intermediate (2,935)	Low (947)
Nest density (nests/ha.) During 2004-2006	Moderate 6.66/5.33/4.33	High 11/10.33/9/33	High 16/14.33/12.06	Low 0.66/0.66/0.66
Conspicuous period of low floral resources (0 or 1 plant species flowering)	Yes (June – October)	No	No	No
Number of tree species	28	42	59	34
Dominant forest trees	Large numbers of dipterocarps providing resin and gum	Large numbers of dipterocarps providing resin and gum	Large numbers of dipterocarps providing resin and gum	Dipterocarps do not predominate
Number of pollen types foraged	27	32	36	16
Pollen foraged from outside forest type	Yes	No	Yes	Yes

	DDF	UMDF	LMDF	DEF
Number of tree species known to be attractive to stingless bees and their flower color	White (2 species), Yellow (2 species)	White (4 species), Yellow (1 species), Other (3 species)	White (8 species), Other (1 species),	None
Proximity	Close to UMDF		Close to gardens, orchards and human habitation	Close to LMDF
Shape	Long and narrow			
Microclimate	Windy, humid	Humid	Wetter: driest in only 1 month. Milder; hottest or equal hottest in only 2 months	Drier: lowest or equal lowest R.H. in 8 of 12 months. Hotter: hottest or equal hottest in 8 of 12 months
Fire regime	Strongly affected by forest fires (1 or 2 fires per year)	Strongly affected by forest fires	Strongly affected by forest fires	Strongly affected by forest fires

Recommendations

1) Honey baiting (mixed with salt) is an effective and efficient techniques for surveying stingless bees in forest habitats. However, data on nests and pollen foraging are also required for a good understanding of stingless bee communities and their role in pollination.

2) The information presented here offers new insights into the ecology of stingless bees and provides new perspectives that can be applied widely to conservation methods and to strategies for developing native bees as agricultural pollinators. Effective conservation and management strategies will only be possible if data such as presented here are compiled. For example, the process of nest establishment is not yet fully understood. An understanding of this is important both conserving stingless bees in their natural habitat and manipulating them to enhance pollination services to agriculture.

3) The results presented here will provide baseline data on Thailand's bees, which will be essential for monitoring populations in the future. If standardized survey techniques are used, results will be comparable from site to site., and over time.

4) Information acquired in this study forms a basic and supporting knowledge resource for the development of an integrated pollination management program in Thailand.

5) No attempt has been made so far to use molecular methods to study stingless bee taxonomy in Thailand. Our understanding of the stingless bee community at Thong Pha Phum provides an ideal framework for future taxonomic work that might include molecular data (e.g. mitochondrial CO1 data). Other molecular data (e.g. microsatellite data) may provide insight into how closely aggregated colonies are related and thus improve our understanding of how nests are established.

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APPENDICES

APPENDIX A

Key to stingless bees of the Thong Pha Phum District

Note: The following key is based on Sakagami's (1985) key to Sumatran species, published descriptions and specimens collected during the course of the present study. It should not be considered to be definitive and may have limited applicability outside the study region.

Key to genera of stingless bees

1. Forewing length commonly over 4 mm (not always), wing venation usually not greatly reduced. Upper margin of hind tibia with plumose hairs intermixed with simple ones.....**Genus *Trigona***

Forewing length less than 3 mm, wing venation usually greatly reduced. Upper margin of hind tibia without plumose hairs2

2. The malar space almost one-fifth as long as eye, much longer than flagellar diameter.**Genus *Pariotrigona***
 Head and mesosomal dorsum finely and densely punctate, interspaces dimly shining; malar space distinctly wider than width of flagellomere 2; mesoscutellum pale yellow (*Pariotrigona pendleburyi*)

The malar space shorter than flagellar diameter.....**Genus *Lisotrigona***
 Head and mesosomal dorsum with punctures sparser and interspaces more lustrous; malar space narrower than width of flagellomere 2; mesoscutellum black (*Lisotrigona cacciae*)

Key to species of stingless bee (Genus *Trigona*)

1. Head and thorax either entirely smooth and polished, or with sculpturing so sparse and delicate that the shininess of the surface is usually dulled only, if at all by the presence of hairs..... **3**

Head and mesosoma dorsally coriaceous or tessellate, not shining; mesoscutum peripherally covered with scale-like tomentum; wing venation less reduced and pterostigma narrower; medium to large species.....**2**

2. Small bee species, body length less than 4.3 mm, fore wing length less than 4.5 mm; tomentum of mesoscutum usually whitish and not extending to mesoscutellum; hind tibia not apically much expanded; basal metasomal terga not contrasting in color with more posterior terga, but with dark markings.....
..... *ventralis*

Larger bee species body length greater than 5.5 mm, fore wing length greater than 4.8 mm; tomentum of mesoscutum bright yellow brown and extending to mesoscutellum; hind tibia apically more expanded; basal metasomal terga pale ferruginous to ivory colored, contrasting with more posterior terga, with small, dark markings
..... *terminata*

3. Propodeum dorsally covered with woolly hairs; mandibular teeth strong; robust species, body length more than 7 mm, fore wing more than 7.3 mm
..... *canifrons*

Propodeum not woolly, dorsally shiny..... **4**

4. Mesoscutellum projecting backward, exceeding posterior slope of propodeum; malar space linear or at most shorter than $\frac{1}{2}$ width of flagellomere 2..... 5
- 5
- Mesoscutellum not projecting beyond posterior slope of propodeum; malar space as long as width of flagellomere 2 7
5. Hind basitarsus wider than $\frac{2}{3}$ width of hind tibia; malar space very long, more than 2.0 width of flagellomere 2; submarginal cells less reduced; large species, body length more than 6.9 mm, fore wing length more than 8.4 mm; body dark brown to black with extensive reddish markings..... *thoracica*
- Hind basitarsus not wider than $\frac{1}{2}$ width of hind tibia; malar space as long as width of flagellomere 2 or or less. submarginal cells indistinct or obsolete.....6
6. Malar space about as long as width of flagellomere 2; body color lighter, hind tibia and basitarsus more slender *apicalis*
- Malar space less than width of flagellomere 2, ratio about 5:7; body color darker ; hind tibia and basitarsus more stout..... *melanoleuca*
7. Fore wings brown, reddish brown or dark brown at base, contrasting with milk white or hyaline apical half..... 8
- Fore wings *either* uniformly hyaline, *or* uniformly and weakly darkened, *or* basally fusco-hyaline with remainder of wing flavo-hyaline..... 9
8. Head reddish yellow; mesoscutum reddish yellow; mesopleuron sparsely hairy posteriorly; hind tibia more slender *atripes*

Head dark brown; mesoscutum dark; mesopleuron densely hairy posteriorly; hind tibia wider *collina*

9. Body entirely pale brown; head, mesoscutum usually honey colored to ferruginous; forewing hyaline; body length 4.92–5.10 mm; fore wing length 5.20 – 5.35 mm..... *melina*

Body brown to black; head , mesoscutum reddish brown to black; forewing hyaline or uniformly darkened **10**

10. Small bee species, body and fore wing lengths both less than 3.5 mm; mesoscutal glabrous areas especially lateral one (G3) conspicuous; scape yellow.....
.....*fuscobalteata*

Larger bee species, body length greater than 6.0 mm, fore wing length greater than 7.3 mm; mesoscutal glabrous areas especially lateral one (G3) inconspicuous; scape dark **11**

11. Head black; scape testaceous; mesosoma pale yellowish brown or testaceous, except scutum black with sharply defined, lateral, reddish areas; integument largely shining and impunctate..... **12**

Head brown to dark brown; scape predominantly yellow; mesosoma not as in alternate, either mesoscutum and mesoscutellum both black or mesoscutum black and mesoscutellum pale yellow or mesoscutellum dark brown and mesoscutellum black *pagdeni*

12. Mesopleuron predominantly reddish brown , lower third with black, anteroventral mark *sirindhornae*

Mesopleuron uniformly black **new species (*Trigona* sp. 1)**

APPENDIX B

Appendix B Table 1 List of stingless bee species (Genus *Trigona*, *Pariotrigona* and *Lisotrigona*) found in Thailand

Species of stingless bees	Schwarz (1939)	Sakagami <i>et al.</i> (1985)	Saiboon (1996)	Rajitparinya (2003)	Michener& Boongird (2004)	Wattanachai Yingchareon <i>et al.</i> (2004)	Klalasikorn <i>et al.</i> (2005)	Inson & Malaipan (2006)
<i>T. aliciae</i> Cockerell	*							
<i>T. apicalis</i> Smith	*	*	*	*		*		*
<i>T. atripes</i> Smith		*	*					*
<i>T. bighami</i> Schwarz	*						*	
<i>T. canifrons</i> Smith		*						*
<i>T. collina</i> Smith	*			*		*		*
<i>T. doipaensis</i> Schwarz	*	*						
<i>T. ferrea</i> Cockerell	*							
<i>T. fimbriata</i> Smith	*	*		*		*		
<i>T. flavibasis</i> Cockerell	*							*
<i>T. fuscibasis</i> Cockerell		*						*
<i>T. fuscobalteata</i> Cameron	*	*	*			*		
<i>T. geissleri</i> Cockerell	*	*						*
<i>T. hirashimai</i> Schwarz		*						
<i>T. iridipennis</i> Smith	*							

Appendix B Table 1 (Continued)

Species of stingless bees	Schwarz (1939)	Sakagami <i>et al.</i> (1985)	Saiboon (1995)	Rajitparinya (2003)	Michener& Boongrid (2004)	Wattanachai yingchareon (2004)	Klalasikorn (2005)	Inson & Malaipan (2006)
<i>T. itama</i> Cockerell		*	*					
<i>T. latigentalis</i> Cockerell	*	*				*		
<i>T. laeviceps</i> Smith		*	*	*		*		
<i>T. melanoleuca</i> Cockerell	*	*		*				*
<i>T. melina</i> Gribodo	*	*						
<i>T. minor</i> Sakagami							*	
<i>T. nitidiventris</i> Smith		*						
<i>T. pagdeni</i> Schwarz	*	*						
<i>T. pagdeniformis</i> Sakagami		*						
<i>T. peninsularis</i> Cockerell	*	*						
<i>T. sarawakensis</i> Cockerell	*							
<i>T. sirindhornae</i> Michener & Boongrid					*			
<i>T. terminata</i> Smith	*		*	*		*		*
<i>T. thoracica</i> Smith		*	*					*
<i>T. valdezi</i> Cockerell	*							

Appendix B Table 1 (Continued)

Species of stingless bees	Schwarz (1939)	Sakagami <i>et al.</i> (1985)	Saiboon (1995)	Rajitparinya (2000)	Michener& Boongrid (2004)	Wattanachai yingchareon (2004)	Klalasikorn (2005)	Inson & Malaipan (2006)
<i>T. ventralis</i> Smith	*	*	*					*
<i>L. cacciae</i> (Nurse) ¹	*	*	*	*				*
<i>P. pendleburyi</i> (Nurse)			*					*
<i>L. klossi</i>								*
<i>L. furva</i>								
Total	21	22	10	7	21	7	10	11

Lisotrigona a senior synonym of *Hypotrigona* , ¹ Senior synonym of *Hypotrigona scintillans* (= *Lisotrigona cacciae*)

Appendix B Table 2 Analysis of variance in DDF

ANALYSIS OF VARIANCE FOR X1

SV	DF	SS	MS	F
REP (R)	29	57.170833	1.971408	<1
TREATED (T)	7	3441.729197	491.675595	126.92 **
ERROR	203	786.395833	3.873871	
TOTAL	239	4285.295833		

CV = 43.2%

** = Significant at 1% level

TABLE OF TREATED (T) MEANS FOR X1
(AVE. OVER 30 REPS)

TREATMENTS	RANKS	MEANS
T1 (SaS)	6	2.5 d
T2 (SuS)	4	5.2 c
T3 (HS)	2	12.2 b
T4 (HSaS)	1	22.0 a
T5 (FSa)	3	5.9 c
T6 (YPT)	5	3.0 c
T7 (WPT)	8	2.1 d
T8 (BPT)	7	2.2 d
MEAN		6.9

Appendix B Table 3 Analysis of variance in UMDF

ANALYSIS OF VARIANCE FOR X1

SV	DF	SS	MS	F
REP (R)	29	214.920933	7.411063	1.36 ns
TREATED (T)	7	3696.629167	528.089881	96.99 **
ERROR	203	1105.245833	5.444561	
TOTAL	239	5016.795833		

CV = 46.4%
 ** = Significant at 1% level; ns: not significant

TABLE OF TREATED (T) MEANS FOR X1
 (AVE. OVER 30 REPS)

TREATMENTS	RANKS	MEANS
T1 (SaS)	6	2.1 d
T2 (SuS)	4	4.6 c
T3 (HS)	2	9.8 b
T4 (HSaS)	1	13.1 a
T5 (FSa)	3	4.6 c
T6 (YPT)	5	2.3 d
T7 (WPT)	8	1.8 d
T8 (BPT)	7	2.0 d
MEAN		5.0

Appendix B Table 4 Analysis of variance in LMDF

ANALYSIS OF VARIANCE FOR X1

SV	DF	SS	MS	F
REP (R)	29	57.170833	1.971408	<1
TREATED (T)	7	3441.729197	491.675595	126.92 **
ERROR	203	786.395833	3.873871	
TOTAL	239	4285.295833		

CV = 43.2%

** = Significant at 1% level

TABLE OF TREATED (T) MEANS FOR X1
(AVE. OVER 30 REPS)

TREATMENTS	RANKS	MEANS
T1 (SaS)	7	1.6 d
T2 (SuS)	3	4.3 c
T3 (HS)	2	9.6 b
T4 (HSaS)	1	12.0 a
T5 (FSa)	4	3.6 c
T6 (YPT)	6	1.7 d
T7 (WPT)	6	1.7 d
T8 (BPT)	5	1.9 d
MEAN		4.6

Appendix B Table 5 Analysis of variance in DEF

ANALYSIS OF VARIANCE FOR X1

SV	DF	SS	MS	F
REP (R)	29	91.2875000	3.1478448	1.67 *
TREATED (T)	7	143.8291667	20.5470238	10.90 **
ERROR	203	382.5458333	1.8844622	
TOTAL	239	617.6625000		

CV = 43.2%

** = Significant at 1% level; * = significant at 5 % level

TABLE OF TREATED (T) MEANS FOR X1
(AVE. OVER 30 REPS)

TREATMENTS	RANKS	MEANS
T1 (SaS)	7	0.6 c
T2 (SuS)	2	1.9 b
T3 (HS)	3	1.9 b
T4 (HSaS)	1	2.9 a
T5 (FSa)	4	1.2 c
T6 (YPT)	5	0.8 c
T7 (WPT)	6	0.7 c
T8 (BPT)	5	0.8 c
MEAN		1.3

Appendix B Table 6 Types of stingless bee and number of individuals visiting honey-bait traps from four types of forest during April 2004 to March 2005.

Rank	species	Number of individuals				Total
		DDF	UMDF	LMDF	DEF	
1	<i>T. ventralis</i>	3,907	1,212	694	0	5,813
2	<i>T. sirindhornae</i>	1,514	1,324	600	153	3,591
3	<i>T. collina</i>	215	793	549	108	1,665
4	<i>T. terminata</i>	777	397	315	0	1,489
5	<i>T. apicalis</i>	293	32	140	282	747
6	<i>P. pendleburyi</i>	187	197	121	142	647
7	<i>L. cacciae</i>	252	124	75	0	451
8	<i>T. thoracica</i>	0	0	170	262	432
9	<i>T. canifrons</i>	279	0	0	0	279
10	<i>T. melina</i>	0	0	271	0	271
11	<i>T. fuscobalteata</i>	4	0	0	0	4
Total		7,428	4,079	2,933	947	15,389

Appendix B Table 7 Types of stingless bee and number of individuals visiting
Honey-bait traps from four types of forest during dry season.

Rank	species	Number of individuals				Total
		DDF	UMDF	LMDF	DEF	
1	<i>T. ventralis</i>	2,228	848	526	0	3,602
2	<i>T. sirindhornae</i>	1,396	986	441	117	2,940
3	<i>T. collina</i>	167	515	361	88	1,131
4	<i>T. terminata</i>	589	354	232	0	1,175
5	<i>T. apicalis</i>	282	29	87	188	586
6	<i>P. pendleburyi</i>	146	145	84	101	476
7	<i>L. cacciae</i>	187	108	68	0	363
8	<i>T. thoracica</i>	0	0	113	182	295
9	<i>T. canifrons</i>	239	0	0	0	239
10	<i>T. melina</i>	0	0	183	0	183
11	<i>T. fuscobalteata</i>	4	0	0	0	4
Total		5,238	2,985	2,095	676	10,994

Appendix B Table 8 Types of stingless bee and number of individuals visiting honey-bait traps from four type of forest during wet season.

Rank	Species	Number of individuals				
		DDF	UMDF	LMDF	DEF	Total
1	<i>T. ventralis</i>	1,679	364	168	0	2,211
2	<i>T. sirindhornae</i>	118	338	159	36	651
3	<i>T. collina</i>	48	278	188	20	534
4	<i>T. terminata</i>	188	43	83	0	314
5	<i>T. apicalis</i>	11	3	53	94	161
6	<i>P. pendleburyi</i>	41	52	37	41	171
7	<i>L. cacciae</i>	65	16	7	0	88
8	<i>T. thoracica</i>	0	0	57	80	137
9	<i>T. canifrons</i>	40	0	0	0	40
10	<i>T. melina</i>	0	0	88	0	88
11	<i>T. fuscobalteata</i>	0	0	0	0	0
Total		2,190	1,094	840	271	4,395

Appendix B Table 9 Taxonomic composition, scientific names affiliation of nest trees of stingless bees in four types of forest.

Type of forest	Scientific names of trees	Family	No. trees	Dbh	Scientific name of stingless bee	No. of bee nests
DDF	<i>Shorea obtusa</i> Wall ex Blume	Dipterocarpaceae	2	152	<i>T. apicalis</i>	1
					<i>Trigona</i> sp.1	1
	<i>S. siamensis</i> Miq	Dipterocarpaceae	3	180	<i>L. cacciae</i>	1
					<i>T. ventralis</i>	2
					<i>Trigona</i> sp.1	2
	<i>Dipterocarpus obtusifolius</i> Teijsm. Ex. Robx	Dipterocarpaceae	1	210	<i>T. sirindhornae</i>	4
<i>D. tuberculatus</i> Robx.	Dipterocarpaceae	2	190	<i>P. pendleburyi</i>	1	
				<i>T. ventralis</i>	3	
<i>Lithocarpus aggregatus</i> Barnett	Fagaceae	1	175	<i>T. apicalis</i>	1	
				<i>P. pendleburyi</i>	1	
<i>L. calathiformis</i> Rehder & Wilson	Fagaceae	1	189	<i>Trigona</i> sp.1	1	
				<i>P. pendleburyi</i>	1	

Appendix B Table 9 (Continued)

Type of forest	Scientific names of trees	Family	No. trees	Dbh	Scientific names of stingless bee	No. of bee nests
UMDF	<i>Ficus</i> sp. Blume	Moraceae	1	360	<i>T. collina</i>	3
					<i>T. ventralis</i>	8
					<i>T. terminata</i>	8
					<i>T. sirindhornae</i>	2
					<i>T. apicalis</i>	1
					<i>T. pagdeni</i>	3
					<i>T. fuscobalteata</i>	1
<i>P. pendleburyi</i>	1					
	<i>Dipterocarpus costatus</i> C.F. Gaerth	Dipterocarpaceae	1	198	<i>T. sirindhornae</i>	1
	<i>Xylia xylocarpa</i> var. <i>kerrii</i> (Robx.) Taub.	Leguminosae	1	220	<i>Trigona</i> sp.1	1
	<i>Anogeissus acuminata</i> Kurz	Dipterocarpaceae	1	230	<i>Trigona</i> sp.1	1
LMDF	<i>Ficus benjamina</i> L.	Moraceae	1	390	<i>T. apicalis</i>	1
					<i>T. melanoleuca</i>	1
					<i>T. sirindhornae</i>	2
					<i>T. collina</i>	1
					<i>T. terminata</i>	3
					<i>L. cacciae</i>	1

Appendix B Table 9 (Continued)

Type of forest	Scientific names of trees	Family	No. trees	Dbh	Scientific names of stingless bee	No. of bee nests
	<i>Garuga pinnata</i> Roxb.	Burseraceae	1	256	<i>T. collina</i> <i>T. ventralis</i> <i>T. terminata</i> <i>T. sirindhornae</i> <i>T. apicalis</i> <i>T. canifrons</i>	3 2 2 3 1 1
	<i>Ficus</i> sp.1	Moraceae	1	188	<i>T. terminata</i> <i>T. pagdeni</i>	1 1
	<i>Lagerstroemia tomentosa</i> C. Presl	Lythraceae	1	195	<i>T. thoracica</i>	1
	<i>Azelia xylocarpa</i> Kurz	Leguminosae	1	248	<i>T. pagdeni</i> <i>T. melanoleuca</i>	1 1
	<i>Hydnocarpus sumatrana</i> (Miq.) Koord	Flacourtiaceae	1	194	<i>T. melanoleuca</i>	1

Appendix B Table 9 (Continued)

Type of forest	Scientific names of tree	Family	No. trees	Dbh	Scientific names of stingless bee	No. of bee nests
	<i>Lagerstroemia calyculata</i> Kurz	Lythraceae	1	158	<i>T. ventralis</i> <i>T. apicalis</i>	1 1
DEF	<i>L. tomentosa</i> C. Presl	Lythraceae	2	168	<i>T. apicalis</i>	2

Appendix B Table 10 Flowering phenology of plants in dry dipterocarp forest (DDF).

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1	Anacardiaceae	<i>Buchanania lanzan</i> Spreng	*	*	*									*
2	Bignoniaceae	<i>Stereospermum neuranthum</i> Kurz												
3	Caesalpinaceae	<i>Cassia fistula</i> L.			*	*								
4	Crypteroniaceae	<i>Crypteronia paniculata</i> Blume	*										*	*
5	Dileniaceae	<i>Dillenia aurea</i> Sm.		*	*	*	*							
6	Dileniaceae	<i>Dillenia indica</i> L.								*	*			
7	Dipterocarpaceae	<i>Dipterocarpus</i> spp.			*	*	*							
8	Dipterocarpaceae	<i>Dipterocarpus obtusifolius</i> Teijsm. ex Miq.	*	*									*	*
9	Dipterocarpaceae	<i>Dipterocarpus tuberculatus</i> Roxb.	*	*	*	*								*
10	Dipterocarpaceae	<i>Shorea roxburghii</i> G. Don		*	*									
11	Dipterocarpaceae	<i>Shorea obtusa</i> Wall. ex Blume		*	*									
12	Dipterocarpaceae	<i>Shorea siamensis</i> Miq.	*	*	*									
13	Euphobiaceae	<i>Aporosa villosa</i> (Wall. Ex Lindl.) Baill	*	*	*									
14	Fagaceae	<i>Castanopsis indica</i> (Roxb.) A. DC.	*	*	*									
15	Fagaceae	<i>Castanopsis tribuloides</i> (Sm.) A. DC.												
16	Fagaceae	<i>Lithocarpus thomsonii</i> (Miq.) Rehder												
17	Fagaceae	<i>Lithocarpus lindleyanus</i> (Wall)					*	*						
18	Fagaceae	<i>Quercus kerrii</i> Graib		*	*	*								
19	Euphobiaceae	<i>Suregada multiflorum</i> (A. Juss.) Baill.			*	*	*							
20	Guttiferaceae	<i>Cratoxylum formosum</i> (Jack) Dyer	*	*	*	*	*							
21	Lecythidaceae	<i>Careya arborea</i> Roxb.	*	*										*
22	Mimosaceae	<i>Xylia xylocarpa</i> var. <i>keri</i> (Craib&Hutch.) I.C. Nielsen		*	*	*								

Appendix B Table 10 (Continued)

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
23	Papilionoidae	<i>Millettia brandisiana</i> Kurz			*	*								
24	Papilionoidae	<i>Pterocarpus macrocarpus</i> Kurz				*	*							
25	Rubiaceae	<i>Gardenia sootepensis</i> Hutch.			*	*	*	*	*					
26	Rubiaceae	<i>Mitragyna hirsuta</i> Havil												
27	Rubiaceae	<i>Pavetta tomentosa</i> Roxb. Ex. Sm. var <i>tomentosa</i>				*	*							
28	Rubiaceae	<i>Wendlandia tinctoria</i> (Roxb.) DC.	*	*										

Appendix B Table 11 Flowering phenology of plants in lower mixed deciduous forest (LMDF).

No.	Family	Scientific name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1	Annonaceae	<i>Cananga latifolia</i> (Hook.f.&Thomson) Finet&Gagnep.					*	*						
2	Annonaceae	<i>Miliusa velutina</i> (Dunal) Hook.f.&Thomson		*	*	*								
3	Apocynaceae	<i>Wrightia arborea</i> (Dennst.) Mabb.				*	*							
4	Araceae	<i>Amorphophallus</i> sp.				*	*							
5	Asteraceae	<i>Vernonia volkameriifolia</i> (Hosseus)	*	*	*									
6	Bignoniaceae	<i>Fernandoa adenophylla</i> (Wall.ex G. Don) Steenis							*	*	*			
7	Bignoniaceae	<i>Markhamia stipulate</i> Seem. Var. Stipulata		*	*									
8	Bignoniaceae	<i>Oroxylum indicum</i> (L.) Kurz						*	*					
9	Bignoniaceae	<i>Stereospermum neuranthum</i> Kurz					*	*						
10	Bombacaceae	<i>Bombax ceiba</i> L.	*	*	*	*								
11	Burseraceae	<i>Garuga pinnata</i> Roxb	*	*	*									
12	Burseraceae	<i>Protium serratum</i> Engl.	*	*										
13	Caesalpinaceae	<i>Cassia fistula</i> L.		*	*	*	*							
14	Caesalpinoideae	<i>Cassia siamea</i> (Lam.) Irwin&Barneby							*	*				
15	Caesalpindeae	<i>Saraca indica</i> L.	*	*										
16	Celastraceae	<i>Siphonodon celastrineus</i> Griff.					*	*						
17	Combretaceae	<i>Anogeissus acuminata</i> (Roxb. ex DC.) Guill.&Perr.	*	*										
18	Combretaceae	<i>Terminalia alata</i> Heyne ex Roth					*	*						
19	Ebenaceae	<i>Diospyros ehretioides</i> Wall. ex G. Don			*	*								
20	Ebenaceae	<i>Elaeocarpus sphaericus</i> (Gaertn.) K. Schum.			*	*	*							
21	Euphorbiaceae	<i>Croton roxburghii</i> N.P. Balakr.			*									

Appendix B Table 11 (Continued)

No.	Family	Scientific name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
22	Euphorbiaceae	<i>Antidesma acidum</i> Retz.				*	*	*	*					
23	Euphorbiaceae	<i>Antideama ghaesembilla</i> Gaertn.	*	*										
24	Euphorbiaceae	<i>Antidesma sootepense</i> Craib					*	*	*					
25	Euphorbiaceae	<i>Bischofia javanica</i> Blume	*	*										
26	Euphorbiaceae	<i>Cleidion spiciflour</i> (Burm.f.)Merr		*	*									
27	Euphorbiaceae	<i>Phyllanthus emblica</i> L.	*	*	*	*								
28	Euphorbiaceae	<i>Trewia nudiflora</i> L.	*	*	*	*								
29	Flacourtiaceae	<i>Casearia grewiifolia</i> Vent.			*	*	*							
30	Gramineae	<i>Dendrocalamus strictus</i> (Roxb.) Nees		*										
31	Guttiferae	<i>Cratoxylum cochinchinense</i> (Lour.) Blume	*											*
32	Juglandaceae	<i>Engelhardtia spicata</i> Blume var. <i>spicata</i>	*	*										
33	Labiatae	<i>Tectona grandis</i> L.f.						*	*	*	*	*		
34	Lauraceae	<i>Litsea monopetala</i> (Roxb.) Pers.												
35	Lecythidaceae	<i>Careya arborea</i> Roxb.	*	*										*
36	Lytheaceae	<i>Lagerstroemia calyculata</i> Kurz			*	*	*							
37	Lytheaceae	<i>Lagerstroemia tomentosa</i> C. Presl			*	*								
38	Meliaceae	<i>Toona ciliata</i> M. Roem.	*	*										
39	Meliaceae	<i>Terminalia triptera</i> Stapf												
40	Moraceae	<i>Ficus benjamina</i> L.	*	*	*	*								*
41	Moraceae	<i>Ficus</i> spp.		*										
42	Papilionoideae	<i>Dalbergia nigrescens</i> Kurz			*	*								
43	Papilionoideae	<i>Dalbergia cultrata</i> Graham ex Benth		*	*									

Appendix B Table 11 (Continued)

No.	Family	Scientific name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
43	Papilionoideae	<i>Erythrina subumbrans</i> (Hassk.) Merr.	*	*										
44	Papilionoideae	<i>Millettia leucantha</i> Kurz	*	*	*	*								
45	Rhamnaceae	<i>Ziziphus rugosa</i> Lam.		*	*	*								
46	Rubiaceae	<i>Mitragyna diversifolia</i> N.P. Balakr.					*	*						
47	Rubiaceae	<i>Canthium parvifolium</i> Roxb.							*	*				
48	Sabiaceae	<i>Meliosma simplicifolia</i> (Roxb.) Walp.		*	*									
49	Sapindaceae	<i>Dimocarpus longan</i> Lour. Subsp. <i>Longan</i> var. <i>longan</i>		*	*	*								
50	Sapindaceae	<i>Lagerstroemia speciosa</i> (L.) Pers.			*	*								
51	Sapindaceae	<i>Litchi chinensis</i> Sonn.		*	*	*								
52	Sapindaceae	<i>Schleichera oleosa</i> (Lour.) Oken	*	*	*	*								
53	Simaroubaceae	<i>Harrisonia perforata</i> (Blanco) Merr.												
54	Solanaceae	<i>Solanum toivum</i> Sw.												
55	Solanaceae	<i>Solanum mammosum</i> L.												
56	Staphyleaceae	<i>Turpinia pomifera</i> (Roxb.) DC.	*	*	*	*								*
57	Sterculiaceae	<i>Firmiana colorata</i> (Roxb.) R. Br.		*	*									
58	Tiliaceae	<i>Muntingia calabura</i> L.												

Appendix B Table 12 Flowering phenology of plants in upper mixed deciduous forest (UMDF).

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1	Anacardiaceae	<i>Psydrax nitida</i> (Craib) K.M. Wong	*	*	*									
2	Asteaceae	<i>Chromolaena odoratum</i> (L.) R.M. King & H. Rob.	*	*										*
3	Bignoniaceae	<i>Oroxylum indicum</i> (L.) Kurz						*	*					
4	Burseraceae	<i>Garuga pinnata</i> Roxb.	*	*	*									
5	Caesalpiniaceae	<i>Peltophorum dasyrachis</i> (Miq.) Kurz	*	*	*									
6	Celastraceae	<i>Siphonodon celastrineus</i> Griff.					*	*						
7	Combretaceae	<i>Anogeissus acuminata</i> (Roxb. Ex DC.)	*	*										
8	Combretaceae	<i>Terminalia alata</i> Roth					*	*						
9	Combretaceae	<i>Terminalia bellirica</i> (Gaerth.) Roxb.		*	*									
10	Combretaceae	<i>Terminalia triptera</i> Stapf						*	*	*				
11	Dipterocarpaceae	<i>Anisoptera costata</i> Korth.	*	*										*
12	Euphorbiaceae	<i>Aporosa octandra</i> var. <i>yunnanensis</i> (Pax&K. Hoffm)	*	*	*									
13	Euphorbiaceae	<i>Aporosa villosa</i> (Wall. Ex Lindl.) Baill	*	*	*									
14	Euphorbiaceae	<i>Bischofia javanica</i> Blume	*	*										
15	Euphorbiaceae	<i>Croton roxburghii</i> N.P. Balakr.	*	*									*	*
16	Euphorbiaceae	<i>Glochidion sphaerogynum</i> Kurz	*	*			*	*	*	*	*	*	*	*
17	Euphorbiaceae	<i>Mallotus philippensis</i> Mull. Arg.		*	*									
18	Fabaceae	<i>Dalbergia oliveri</i> Gramble	*	*	*	*	*							
19	Flacourtiaceae	<i>Casearia grewiiifolia</i> Vent.												
20	Gentianaceae	<i>Exacum tetragonum</i> Roxb.											*	*

Appendix B Table 12 (Continued)

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
21	Guttiferae	<i>Cratoxylum cochinchinense</i> (Lour.) Blume			*	*	*							
22	Guttiferae	<i>Cratoxylum formosum</i> (Jack)	*	*	*	*	*							
23	Lamiaceae	<i>Callicarpa arborea</i> Roxb.				*	*	*	*					
24	Lamiaceae	<i>Gmelina arborea</i> Roxb.		*	*									
25	Lamiaceae	<i>Vitex peduncularis</i> Wall. Ex Schauer			*	*	*							
26	Lycythidaceae	<i>Barringtonia acutangula</i> (L.) Gaertn.				*	*							
27	Meliaceae	<i>Melia azedarach</i> L.		*	*									
28	Mimosoideae	<i>Albizia odoratissima</i> (L.f.) Benth			*	*	*	*						
29	Mimosoideae	<i>Lannea coromandelica</i> (Houtt.) Merr.			*	*	*							
30	Moraceae	<i>Ficus</i> spp.		*										
31	Myrtaceae	<i>Syzygium claviflorum</i> (Roxb.) A.M. Cowan&Cowan			*	*	*							
32	Papilionoideae	<i>Dalbergia oliveri</i> Gramble		*	*	*	*							
33	Papilionoideae	<i>Erythrina subumbrans</i> (Hassk.) Merr.	*	*										
34	Papilionoideae	<i>Millettia brandisiana</i> Kurz			*	*								
35	Papilionoideae	<i>Millettia leucantha</i> Kurz	*	*									*	*
36	Papilionoideae	<i>Pterocarpus macrocarpus</i> Kurz			*	*	*							
37	Rubiaceae	<i>Wendlandia tinctoria</i> (Roxb.) DC.	*	*										
38	Sterculiaceae	<i>Fermiana colorata</i> (Roxb.) R.Br.		*	*									
39	Theaceae	<i>Schima wallichii</i> (DC.) Korth	*	*	*									
40	Tiliaceae	<i>Grewia eriocarpa</i> Juss.			*	*	*	*						
41	Ulamaceae	<i>Trema orientalis</i> (L.) Blume												

Appendix B Table 13 Flowering phenology of plants in dry evergreen forest (DEF).

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1	Anacardiaceae	<i>Mangifera cochinchinensis</i> Engl.												
2	Apocynaceae	<i>Hunteria zeylanica</i> (Retz.) Gardner ex Thwaites		*	*	*	*							
3	Araceae	<i>Alocasia macrorrhizos</i> (L.) G. Don												
4	Celastraceae	<i>Bhesa robusta</i>												
5	Dipterocarpaceae	<i>Dipterocarpus baudii</i> Korth		*	*									
6	Dipterocarpaceae	<i>Dipterocarpus turbinatus</i> C.F. Gaerth												
7	Dipterocarpaceae	<i>Parashorea stellata</i> Kurz	*	*	*									
8	Dipterocarpaceae	<i>Shorea roxburghii</i> G. Don	*	*	*									*
9	Ebenaceae	<i>Diospyros</i> spp.			*	*								
10	Ebenaceae	<i>Diospyros da syphylla</i> Kurz			*	*	*							
11	Euphorbiaceae	<i>Bridelia retusa</i> (L.) A. Juss					*	*						
12	Fabaceae	<i>Millettia atropurpurea</i> Benth.	*	*	*	*								
13	Lauraceae	<i>Beilschmiedia</i> spp.												
14	Lauraceae	<i>Beilschmiedia assamina</i> Meisn.												
15	Lauraceae	<i>Cinnamomum iners</i> Reinw. ex Blume	*	*										
16	Lauraceae	<i>Cryptocarya pallens</i> Kosterm.												
17	Lythaceae	<i>Lagerstroemia tomentosa</i> C. Presl			*	*								
18	Meliaceae	<i>Aglaiia rubiginosa</i> (Hiern) Pannell							*	*				
19	Meliaceae	<i>Aphanamixis polystachaya</i> (Wall.)				*	*	*						
20	Moraceae	<i>Artocarpus</i> spp.	*			*	*							*
21	Moraceae	<i>Ficus vasculosa</i> Wall. ex Miq.											*	*

Appendix B Table 13 (Continued)

No.	Family	Scientific Name	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
22	Myrtaceae	<i>Knema linifolia</i> (Roxb.) Warb.	*	*										
23	Myrtaceae	<i>Syzygium siamense</i> (Craib.) Chanter. & J. Parn.	*	*										
24	Papilionoideae	<i>Callerya atropurpurea</i> (Wall.) A.M. Schot	*	*	*	*								
25	Papilionoideae	<i>Millettia leucantha</i> Kurz	*	*										*
26	Rubiaceae	<i>Aglaia</i> sp.				*	*	*						
27	Rubiaceae	<i>Ceriscoides turgida</i> (Roxb.) Tirveng												
28	Rubiaceae	<i>Mitragyna hirsuta</i> Havil												
29	Rubiaceae	<i>Pavetta tomentosa</i> Robx.ex Sm. Var. tomentosa				*	*							
30	Sapindaceae	<i>Payena</i> spp. (<i>Mimusops elengi</i> Linn.)	*	*	*	*	*	*	*	*	*	*	*	*
31	Sapindaceae	<i>Xerospermum noronhianum</i> (Blume) Blume										*	*	
32	Sapotaceae	<i>Palaquium</i> spp.												
33	Sterculiaceae	<i>Pterospermum acerifolium</i> (L.) Willd												
34	Sterculiaceae	<i>Pterocymbium tinctorium</i> (Blanco) Merr.		*	*									

Appendix B Table 14 Morphology of flowers visited by stingless bees.

No	Family	Scientific Name	Type of forest	Flower type						Size of flower			Color			Species of stingless bees	
				Inflorescence	Aestivation	corolla tube	calyx tube	Open	Close	S	M	L	White	Yellow	Others		
1	Annonaceae	<i>Annona squamosa</i>	LMDF	Head	Valvate	-	T	*		*		*					ap,co
2	Burseraceae	<i>Garuga pinnata</i>	UMDF	Panicle	Imbricate	Free	T	*			*		*			orange	ap,co
3	Caesalpiaceae	<i>Saraca indica</i>	LMDF	Panicle	Imbricate	-	-	*			*						ap,co,ve
4	Elaeocarpaceae	<i>Elaeocarpus hygrophilus</i>	LMDF	Panicle	Imbricate	-	-	*		*		*				violet	ap,co,ve
5	Euphorbiaceae	<i>Antidesma sootepense</i>	UMDF	Panicle	Imbricate	-	T	*			*					pink	ap,co,ve
6	Guttiferae	<i>Gratoxylum formosum</i>	UMDF	Panicle	Imbricate	-	T	*			*					pink	ap,co,ve
7	Mimosaceae	<i>Mimosa pudica</i>	LMDF	Head	Valvate	Free	T	*			*						ap,co,ve
8	Lythraceae	<i>Lagerstroemia tomentosa</i>	LMDF	Raceme	Imbricate	-	T	*			*		*				ap,co,ve
9	Meliaceae	<i>Melia azedarach</i>	UMDF	Panicle	Imbricate	-	-	*		*		*					ap,co,ve
10	Mimosaceae	<i>Parkia speciosa</i>	LMDF	Panicle	Valvate	Free	T	*			*		*				ap,co
11	Sapindaceae	<i>Schleichera oleosa</i>	LMDF	Panicle	Imbricate	-	-	*			*		*				ap,co,ve,te,si
12	Sapindaceae	<i>Dimocarpus longan</i>	LMDF	Solitary	Imbricate	-	-	*			*		*				ap,co,ve,te
13	Tiliaceae	<i>Muntingia calabura</i>	LMDF	Solitary	Imbricate	-	-	*		*		*					ap,co,ve
14	Dilleniaceae	<i>Dillenia</i> sp.	DDF	Solitary	Imbricate	-	-	*				*		*			ap,co,ve
15	Dilleniaceae	<i>Dillenia parviflora</i>	DDF	Panicle	Imbricate	-	-	*				*		*			ap,co,ve
16	Dipterocarpaceae	<i>Hopea</i> .sp	DDF	Panicle	Contorse	-	-	*		*		*					ap,co,ve
17	Fagaceae	<i>Lithocarpus thomsonii</i>	DDF	Panicle	Imbricate	-	-	*		*		*					ap,co,ve
18	Lamiaceae	<i>Tectona grandis</i>	LMDF	Panicle	Imbricate	Free	T	*		*		*					ap,co,ve
19	Lamiaceae	<i>Vitex peduncularis</i>	UMDF	Panicle	Imbricate	Free	T	*		*		*					ap,co,ve
20	Fabaceae	<i>Dalbergia obovatai</i>	UMDF	Panicle	Imbricate	-	T		*	*		*					ap,co,ve,te,si
21	Fabaceae	<i>Dalbergia oliveri</i>	UMDF	Panicle	Imbricate	-	T		*			*					ap,co,ve,te,si

ap = *Trigona apicalis*
ve = *Trigona ventralis*
si = *Trigona sirindhornae*

co = *Trigona collina*
te = *Trigona terminata*

Appendix B Table 15 Flowering phenology of plants that stingless bee collected pollen.

No.	Family	Scientific Name	Type of forest	Distance (Metre)	Month (January-December)												Species of stingless bees
					1	2	3	4	5	6	7	8	9	10	11	12	
1	Acanthaceae		DDF		*	*		*							*	ap	
2	Acantraceae		DDF		*	*		*							*	ap	
3	Acanthaceae		DEF		*	*				*		*	*	*	*	ap	
4	Acanthaceae		DDF							*						ap	
5	Amaryllidaceae		LMDF		*	*				*	*		*	*	*	co	
6	Amaryllidaceae1		LMDF		*	*					*	*	*	*	*	me	
7	Annonaceae	<i>Annona squamosa</i>	LMDF	800-1,200	*	*										ap,ca,ve	
8	Araceae		DEF		*	*		*	*						*	ap	
9	Araceae		LMDF									*	*	*	*	ap,ca	
10	Asteraceae		UMDF		*							*	*	*	*	te	
11	Asteraceae		UMDF								*	*	*			te	
12	Asteraceae		DEF		*	*	*	*							*	ap	
13	Asteraceae1		DEF							*	*	*		*		ap	
14	Bignoniaceae		LMDF							*	*	*	*	*	*	co,ve	
15	Burseraceae		UMDF							*	*	*				te	
16	Burseraceae	<i>Caruga pinnata</i>	UMDF	850		*	*	*								ap,co,te	
17	Caesalpiniaceae	<i>Saraca indica</i>	LMDF	950	*	*							*	*	*	ap,ca,ve	
18	Caesalpiniaceae		UMDF		*							*	*	*	*	ap	
19	Caesalpiniaceae		DDF							*						ap	
20	Caesalpiniaceae		DDF								*					ap	
21	Caesalpiniaceae		DDF								*					ap	
22	Caesalpiniaceae		DEF				*	*				*	*	*		ap	
23	Caesalpiniaceae		DEF									*	*	*		ap	
24	Caesalpiniaceae		LMDF					*								ca	

Appendix B Table 15 (Continued)

No.	Family	Scientific Name	Type of forest	Distance	Month (January-December)												Species of stingless bees
					1	2	3	4	5	6	7	8	9	10	11	12	
25	Caprifoliaceae		LMDF		*	*						*	*	*	*	*	co
26	Compositae		DEF				*	*									ap
27	Compositae		LMDF		*	*						*	*	*	*	*	co,me
28	Convolvulaceae		LMDF		*	*				*		*	*	*	*	*	me
29	Costaceae		LMDF		*	*				*		*	*	*	*	*	me
30	Cucurbitaceae		LMDF		*	*	*	*								*	me
31	Convolvulaceae		LMDF									*	*	*	*	*	ap
32	Dilleniaceae	<i>Dillenia</i> sp.	DDF	900								*	*	*			ap
33	Dilleniaceae	<i>Dillenia parviflora</i>	DDF	975								*	*	*			ap
34	Dipterocarpaceae	<i>Hopea</i> sp.	DDF	1,390	*	*	*									*	ap
35	Elaeocarpaceae	<i>Elaeocarpus hygrophilus</i>	LMDF	1,100	*	*		*	*	*							ap,co,ve
36	Euphorbiaceae		DDF		*	*										*	ap
37	Euphorbiaceae		DDF					*									ap
38	Euphorbiaceae		DDF					*									ap
39	Euphorbiaceae		DEF				*	*	*								ap
40	Euphorbiaceae	<i>Antidesma sootepense</i>	UMDF	975				*	*	*							ap,te
41	Fabaceae	<i>Dalbergia</i> sp.	UMDF	800	*	*	*	*	*								ap,co,te,ve
42	Fabaceae	<i>Dalbergia parviflora</i>	UMDF	870	*	*	*							*			ap,co,te,ve
43	Fabaceae		DDF			*											ap
44	Fabaceae		DDF						*								ap
45	Fabaceae	<i>Mimosa pudica</i>	LMDF	300-900								*	*	*	*	*	ap,ca,si
46	Fagaceae	<i>Lithocarpus thomsonii</i>	DDF	1,375	*	*	*	*									ap
47	Guttiferae	<i>Cratoxylum formosum</i>	UMDF	1,190	*	*	*	*								*	ap,co,te,ve
48	Hydrangeaceae		LMDF		*											*	me

Appendix B Table 15 (Continued)

No.	Family	Scientific Name	Type of forest	Distance	Month (January-December)												Species of stingless bees
					1	2	3	4	5	6	7	8	9	10	11	12	
49	Lamiaceae		DEF		*	*				*	*		*	*	*	ap	
50	Lamiaceae	<i>Vitex peduncularis</i>	UMDF	1,350		*	*	*	*			*				co	
51	Lythaceae	<i>Lagerstroemia tomentosa</i>	LMDF	1,100		*	*	*								ap,co,ca,ve	
52	Magnoliaceae		LMDF		*		*	*	*					*	*	me	
53	Malvaceae		LMDF								*	*	*	*	*	ve	
54	Mimosaceae		DEF				*	*	*							ap	
55	Meliaceae	<i>Melia azedarach</i>	UMDF	950	*	*	*								*	ap,co,te	
56	Mimosaceae	<i>Parkia speciosa</i>	LMDF	750				*	*							ap,ca	
57	Mimosaceae		UMDF											*	*	ap,te	
58	Oleaceae		LMDF		*	*					*	*	*	*	*	ve	
59	Oleaceae1		LMDF		*	*				*		*		*	*	ve	
60	Passifloraceae		LMDF		*			*	*				*	*		me	
61	Rubiaceae		DDF								*	*				ap	
62	Salanaceae		LMDF		*	*					*	*		*	*	ve	
63	Sapindaceae	<i>Schleichera oleosa</i>	LMDF	650			*	*	*	*						ap,co,me,ca,si	
64	Sapindaceae	<i>Dimocarpus longan</i>	LMDF	600-1,450	*	*	*	*				*	*	*		ap,co,me,ca,ve,si	
65	Tiliaceae	<i>Muntingia calabura</i>	LMDF	890	*	*	*	*								ap,co,me,ca,ve	
66	Tiliaceae		LMDF		*	*			*					*	*	ve	
67	Verbenaceae		LMDF		*	*		*	*	*		*	*	*	*	me	
68	Verbenaceae		DDF									*	*			ap	
69	Verbenaceae		DDF				*									ap	
70	Lamiaceae	<i>Tectona grandis</i>	LMDF	600-1,150						*	*	*	*	*	*	ap,co,ca,ve,si	
71	Unknown 1		DDF				*									ap	
72	Unknown 2		DDF		*	*										ap	

Appendix B Table 15 (Continued)

No.	Family	Scientific Name	Type of forest	Distance	Month (January-December)												Species of stingless bees
					1	2	3	4	5	6	7	8	9	10	11	12	
73	Unknown	3	DDF		*	*									*	*	ap
74	Unknown	4	DDF				*			*			*	*	*	*	ap
75	Unknown	5	DDF						*			*	*	*	*	*	ap
76	Unknown	6	DDF						*				*	*	*	*	ap
77	Unknown	7	DDF		*					*			*	*	*	*	ap
78	Unknown	8	DDF		*			*					*	*			ap
79	Unknown	9	UMDF						*								te
80	Unknown	10	UMDF		*				*			*	*	*	*	*	te
81	Unknown	11	UMDF		*			*	*	*	*	*	*	*	*	*	co
82	Unknown	12	UMDF		*							*	*	*	*	*	te
83	Unknown	13	UMDF		*				*	*	*	*	*	*	*	*	co
84	Unknown	14	UMDF					*									te
85	Unknown	15	UMDF					*									te
86	Unknown	16	UMDF		*		*	*		*	*	*	*	*	*	*	ap
87	Unknown	17	UMDF		*		*			*	*	*	*	*	*	*	ap
88	Unknown	18	UMDF				*						*	*	*	*	ve
89	Unknown	19	UMDF				*						*	*	*	*	ve
90	Unknown	20	UMDF		*		*		*	*	*	*	*	*	*	*	ap
91	Unknown	21	UMDF		*	*					*	*	*	*	*	*	ap
92	Unknown	22	UMDF		*	*		*		*	*	*	*	*	*	*	co
93	Unknown	23	UMDF				*	*					*	*	*	*	ve
94	Unknown	24	UMDF					*				*	*	*	*	*	ve
95	Unknown	25	UMDF		*	*				*	*	*	*	*	*	*	ap
96	Unknown	26	UMDF						*		*	*	*	*	*	*	ve

Appendix B Table 15 (Continued)

No.	Family	Scientific Name	Type of forest	Distance	Month (January-December)												Species of stingless bees
					1	2	3	4	5	6	7	8	9	10	11	12	
97	Unknown	27	UMDF							*	*	*	*	*		ve	
98	Unknown	28	UMDF								*	*	*	*		ve	
99	Unknown	29	LMDF		*	*	*	*	*	*				*	*	ap,me,ca,si	
100	Unknown	30	LMDF		*	*		*	*	*				*	*	ap,ca	
101	Unknown	31	LMDF			*					*	*	*	*	*	ap,ca,si	
102	Unknown	32	LMDF		*	*					*	*	*	*	*	ap,ca,si	
103	Unknown	33	LMDF		*	*								*	*	ap,ca	
104	Unknown	34	LMDF		*	*		*	*	*	*		*	*	*	co,ve,si	
105	Unknown	35	LMDF		*	*		*	*	*	*		*	*	*	co,ve,si	
106	Unknown	36	DEF						*	*						ap	
107	Unknown	37	DEF				*	*	*							ap	
108	Unknown	38	DEF		*	*			*		*	*	*	*	*	ap	
109	Unknown	39	DEF		*	*					*	*	*	*	*	ap	
110	Unknown	40	DEF		*	*					*	*	*	*	*	ap	
111	Unknown	41	DDF				*									ap	

ap = *Trigona apicalis*
ve = *Trigona ventralis*
ca = *Trigona canifrons*

co = *Trigona collina*
te = *Trigona terminata*

me = *Trigona melina*
si = *Trigona sirindhornae*

Appendix B Table 16 Scientific names and Thai names (Smitinand, 2001) of plants in four types of forest.

Scientific Name	Family	Thai Name
<i>Aglaiia rubiginosa</i> (Hiern) Pannell	Meliaceae	Chomphu samet (ชมพูเสม็ด)
<i>Albizia odoratissima</i> (L.f.) Benth	Mimosoideae	Kang khi mot (กางขี้มอด)
<i>Alocasia macrorrhizos</i> (L.) G. Don	Araceae	Kradat (กระดาด)
<i>Anisoptera costata</i> Korth.	Dipterocarpaceae	Krabak (กระบก)
<i>Annona sguamosa</i>	Annonaceae	Noina (น้อยหน่า)
<i>Anogeissus acuminata</i> (Roxb. ex DC.) Guill. & Perr.	Combretaceae	Ta khian nu (ตากล้าหนู)
<i>Antideama ghaesembilla</i> Gaertn.	Euphorbiaceae	Mao khai pla (เมาไขปลา)
<i>Antidesma acidum</i> Retz.	Euphorbiaceae	Mao soi (เมาสาย)
<i>Antidesma sootepense</i> Craib	Euphorbiaceae	Mamao sai (มะเมาสาย)
<i>Aphanamixis polystachaya</i> (Wall.)	Meliaceae	Ta suea (ตาเสือ)
<i>Aporosa octandra</i> var. <i>yunnanensis</i> (Pax&K. Hoffm)	Euphorbiaceae	Nam phueng khao (น้ำผึ้งขาว)
<i>Aporosa villosa</i> (Wall. Ex Lindl.) Baill	Euphorbiaceae	Lot (โลด)
<i>Barringtonia acutangula</i> (L.) Gaertn.	Lycythidaceae	Chik nam (จิกน้ำ)
<i>Beilschmiedia assamina</i> Meisn.	Lauraceae	Chan dong (จันทน์แดง)
<i>Beilschmiedia</i> spp.	Lauraceae	
<i>Bhesa robusta</i> (Roxb.)	Celastraceae	Kradong daeng (กระโดงแดง)
<i>Bischofia javanica</i> Blume	Euphorbiaceae	Toem (เต็ม)
<i>Bischofia javensis</i> Blume	Euphorbiaceae	Toem (เต็ม)
<i>Bombax ceiba</i> L.	Bombacaceae	Ngio ban (จิวบ้าน)
<i>Bridelia retusa</i> (L.) A. Juss	Euphorbiaceae	Teng nam (เต็งหนาม)
<i>Buchanania lanzan</i> Spreng	Anacardiaceae	Mamuang hua maeng wan (มะม่วงหัวแมงวัน)
<i>Callerya atropurpurea</i> (Wall.) A.M. Schot	Papilionoideae	Kasae (กระแซะ)
<i>Callicarpa arborea</i> Roxb.	Lamiaceae	Cha paen (ชำแป้น)

Appendix B Table 16 (Continued)

Scientific Name	Family	Thai Name
<i>Cananga latifolia</i> (Hook.f. & Thomson) Finet&Gagnep.	Annonaceae	Sakae saeng (สะแกแสง)
<i>Canthium parvifolium</i> Roxb.	Rubiaceae	Nam ma khet (หนามมะเค็ด)
<i>Careya arborea</i> Roxb.	Lecythidaceae	Kradon (กระโดน)
<i>Casearia grewiifolia</i> Vent. var.	Flacourtiaceae	Kruai pa (กรวยป่า)
<i>Cassia fistula</i> L.	Caesalpinaceae	Ratcha pruek (ราชพฤกษ์)
<i>Cassia siamea</i> (Lam.) Irwin&Barneby	Caesalpinioideae	Khi lek (ขี้เหล็ก)
<i>Castanopsis indica</i> (Roxb.) A. DC.	Fagaceae	Ko lim (กอลิม)
<i>Castanopsis tribuloides</i> (Sm.) A. DC.	Fagaceae	Ko bai lueam (กระทงลอย)
<i>Ceriscoides turgida</i> (Roxb.) Tirveng.	Rubiaceae	Krabian (กระเบียน)
<i>Chromolaena odoratum</i> (L.) R.M. King & H. Rob.	Asteaceae	Sap suea (สาปเสื่อ)
<i>Cinnamomum iners</i> Reinw. ex Blume	Lauraceae	Chiat (เขียด)
<i>Cleidion spiciflourum</i> (Burm.f.) Merr	Euphorbiaceae	Dimi (ดีหมี่)
<i>Cratoxylum cochinchinense</i> (Lour.) Blume	Guttiferae	Tio kliang (ต้วเกลี้ยง)
<i>Cratoxylum formosum</i> (Jack) Dyer	Guttiferaceae	Tio Khao (ต้วขาว)
<i>Croton roxburghii</i> N.P. Balakr.	Euphorbiaceae	Plao yai (เปล้าใหญ่)
<i>Crypteronia paniculata</i> Blume	Crypteroniaceae	Kra thong loi (กระทงลอย)
<i>Cryptocarya pallens</i> Kosterm.	Lauraceae	Mak khi ai (หมากขี้ฮ้าย)
<i>Dalbergia cultrata</i> Graham ex Benth	Papilionoideae	Kra phi (กระพี)
<i>Dalbergia nigrescens</i> Kurz	Papilionoideae	Cha nuan, Kra phi (ฉนวน, กระพี)
<i>Dalbergia oliveri</i> Gramble	Fabaceae	Pradu chingchan (ประดู่ ชิงช้าง)
<i>Dendrocalamus strictus</i> (Roxb.) Nees	Gramineae	Sang (ซาง)
<i>Dillenia aurea</i> Sm.	Dilieniaceae	Masan (มะसान)
<i>Dillenia indica</i> L.	Dilieniaceae	Ma tat (มะตาด)
<i>Dillenia parviflora</i>	Dilieniaceae	San hing (सानหิง)

Appendix B Table 16 (Continued)

Scientific Name	Family	Thai Name
<i>Dimocarpus longan</i> Lour. Subsp. <i>Longan</i> var. <i>longan</i>	Sapindaceae	Lamyai (ลำไย)
<i>Diospyros dasyphylla</i> Kurz	Ebenaceae	Chan khao (จันทเข)
<i>Diospyros ehretioides</i> Wall. ex G. Don	Ebenaceae	Tap tao ton (ตับเต๋าดัน)
<i>Dipterocarpus baudii</i> Korth	Dipterocarpaceae	Yang khon (ยางขน)
<i>Dipterocarpus obtusifolius</i> Teijsm. ex Miq.	Dipterocarpaceae	Hiang (เหียง)
<i>Dipterocarpus</i> spp.	Dipterocarpaceae	Yang (ยาง)
<i>Dipterocarpus tuberculatus</i> Roxb.	Dipterocarpaceae	Yang pluang (ยางพลวง)
<i>Dipterocarpus turbinatus</i> C.F. Gaertn	Dipterocarpaceae	Yang daeng (ยางแดง)
<i>Elaeocarpus hygrophilus</i>	Elaeocarpaceae	Ma kok nam (มะกอกน้ำ)
<i>Elaeocarpus sphaericus</i> (Gaertn.) K. Schum.	Ebenaceae	Ma mun dong (มะเมีดง)
<i>Engelhardtia spicata</i> Blume var. <i>spicata</i>	Juglandaceae	Kha hot (คำหุด)
<i>Erythrina subumbrans</i> (Hassk.) Merr.	Papilionoideae	Thong lang pa (ทองหลางป่า)
<i>Exacum tetragonum</i> Roxb.	Gentianaceae	Ya liam (หญ้าเหลียม)
<i>Fernandoa adenophylla</i> (Wall.ex G. Don) Steenis	Bignoniaceae	Khae hang khang (แคหางค่าง)
<i>Ficus benjamina</i> L.	Moraceae	Sai yoi (ไทรย้อย)
<i>Ficus</i> spp.	Moraceae	Sai (ไทร)
<i>Ficus vasculosa</i> Wall. e x Miq.	Moraceae	Ma duea thong (มะเดื่อทอง)
<i>Firmiana colorata</i> (Roxb.) R. Br.	Sterculiaceae	Po fai (ปอฝ้าย)
<i>Gardenia sootepensis</i> Hutch.	Rubiaceae	Khammok luang (คำมอกหลวง)
<i>Garuga pinnata</i> Roxb.	Burseraceae	Ta khram (ตะคร้ำ)
<i>Glochidion sphaerogynum</i> (Mull. Arg.) Kurz	Euphorbiaceae	Man pla (มันปลา)
<i>Gmelina arborea</i> Roxb.	Lamiaceae	So (โสร)
<i>Grewia eriocarpa</i> Juss.	Tiliaceae	Po Kaen thao (ปอแก่นทา)

Appendix B Table 16 (Continued)

Scientific Name	Family	Thai Name
<i>Harrisonia perforata</i> (Blanco) Merr.	Simaroubaceae	Sifan khontha (สีพันคนทา)
<i>Hopea</i> sp.	Dipterocarpaceae	Ta Khain (ตะเคียน)
<i>Hunteria zeylanica</i> (Retz.) Gardner ex Thwaites	Apocynaceae	Muk khao (มุกเขา)
<i>Knema linifolia</i> (Roxb.) Warb.	Myrsicaceae	Lueat kwang (เลือดควาง)
<i>Lagerstroemia calyculata</i> Kurz	Lytheaceae	Ta baek daeng (ตะแบกแดง)
<i>Lagerstroemia speciosa</i> (L.) Pers.	Sapindaceae	Inthanin nam (อินทนิลน้ำ)
<i>Lagerstroemia tomentosa</i> C. Presl	Lytheaceae	Salao khao (เสลาขาว)
<i>Lannea coromandelica</i> (Houtt.) Merr.	Mimosoideae	Kuk (กูก)
<i>Litchi chinensis</i> Sonn.	Sapindaceae	Lin chi (ลิ้นจี่)
<i>Lithocarpus lindleyanus</i> (Wall)	Fagaceae	Ko dang (กอด่าง)
<i>Lithocarpus thomsonii</i> (Miq.) Rehder	Fagaceae	Ko khao (ก้อขาว)
<i>Litsea monopetala</i> (Roxb.) Pers.	Lauraceae	Ka thang (กะทัง)
<i>Mallotus philippensis</i> Mull. Arg.	Euphorbiaceae	Saet (แสต)
<i>Mangifera cochinchinensis</i> Engl.	Anacardiaceae	Mamuang kilen (มะม่วงกิลเลน)
<i>Markhamia stipulata</i> Seem. var. <i>stipulata</i>	Bignoniaceae	Khae hua mu (แคค้างหมู)
<i>Melia azedarach</i> L.	Meliaceae	Lian (เลี่ยน)
<i>Meliosma simplicifolia</i> (Roxb.) Walp.	Sabiaceae	Duea hu kwang (เดื่อหูกวาง)
<i>Miliusa velutina</i> (Dunal) Hook.f.&Thomson	Annonaceae	Kongkang, Hang rok (โกงกาง, หางรอก)
<i>Millettia brandisiana</i> Kurz	Papilionoideae	Phi chan (พี้จัน)
<i>Millettia brandisiana</i> Kurz	Papilionoidae	Kra phi chan (กระพี้จัน)
<i>Millettia leucantha</i> Kurz var.	Papilionoideae	Kra cho (กระเขาะ)
<i>Mimosa pudica</i>	Mimosaceae	Ra ngap (ระงับ, ไมยราบ)
<i>Mitragyna diversifolia</i> Wall. Ex G. Don	Rubiaceae	Kra thum na (กระทุมนา)
<i>Mitragyna hirsuta</i> Havil	Rubiaceae	Kra thum khok (กระทุมโคก)

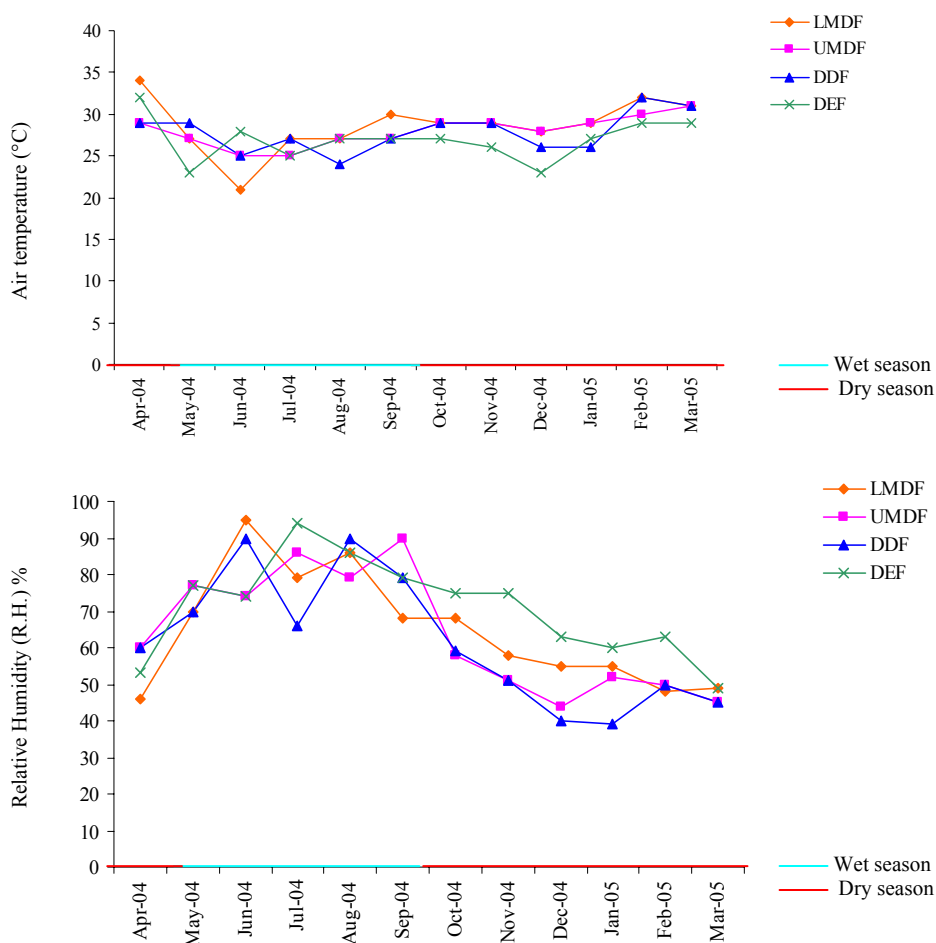
Appendix B Table 16 (Continued)

Scientific Name	Family	Thai Name
<i>Muntingia calabura</i> L.	Tiliaceae	Ta khop farang (ตะขบฝรั่ง)
<i>Oroxylum indicum</i> (L.) Kurz	Bignoniaceae	Pheka (เพกา)
<i>Parashorea stellata</i> Kurz.	Dipterocarpaceae	Khai khiao (ไขเขียว)
<i>Parkia speciosa</i>	Mimosaceae	Sato (สาโท)
<i>Pavetta tomentosa</i> Roxb. Ex. Sm. var <i>tomentosa</i>	Rubiaceae	Khao san pa (ข้าวสารป่า)
<i>Payena</i> spp. (<i>Mimusops elengi</i> Linn.)	Sapindaceae	Phikun (พิกุล)
<i>Peltophorum dasyrachis</i> (Miq.) Kurz	Caesalpiniaceae	A rang (อะราง)
<i>Phyllanthus emblica</i> L.	Euphorbiaceae	Ma kham pom (มะขามป้อม)
<i>Protium serratum</i> Engl.	Burseraceae	Ma faen (มะแฟน)
<i>Psydrax nitida</i> (Craib) K.M. Wong	Anacardiaceae	Kapa (กะปะ)
<i>Pterocarpus macrocarpus</i> Kurz	Papilionoideae	Pradu (ประดู่)
<i>Pterocymbium tinctorium</i> (Blanco) Merr.	Sterculiaceae	Po i keng (ปออีแกง)
<i>Pterospermum acerifolium</i> (L.) Willd	Sterculiaceae	Kanan pling (กะหนานปลิง)
<i>Quercus kerrii</i> Craib	Fagaceae	Ko phae (ก่อแพะ)
<i>Saraca indica</i> L.	Caesalpindeae	Sok (โศก)
<i>Schima wallichii</i> (DC.) Korth	Theaceae	Mangtan (มังตาน)
<i>Schleichera oleosa</i> (Lour.) Oken	Sapindaceae	Ta khro (ตะดร้า)
<i>Shorea obtusa</i> Wall. ex Blume	Dipterocarpaceae	Teng (เต็ง)
<i>Shorea roxburghii</i> G. Don	Dipterocarpaceae	Phayom (พะยอม)
<i>Shorea siamensis</i> Miq.	Dipterocarpaceae	Rang (รัง)
<i>Siphonodon celastrineus</i> Griff.	Celastraceae	Maduk (มะดุก)
<i>Solanum mammosum</i> L.	Solanaceae	Ma khuea phuang (มะเขือพวง)
<i>Solanum torvum</i> Sw.	Solanaceae	Ma khuea phuang (มะเขือพวง)
<i>Stereospermum neuranthum</i> Kurz	Bignoniaceae	Khae sai (แคทราย)

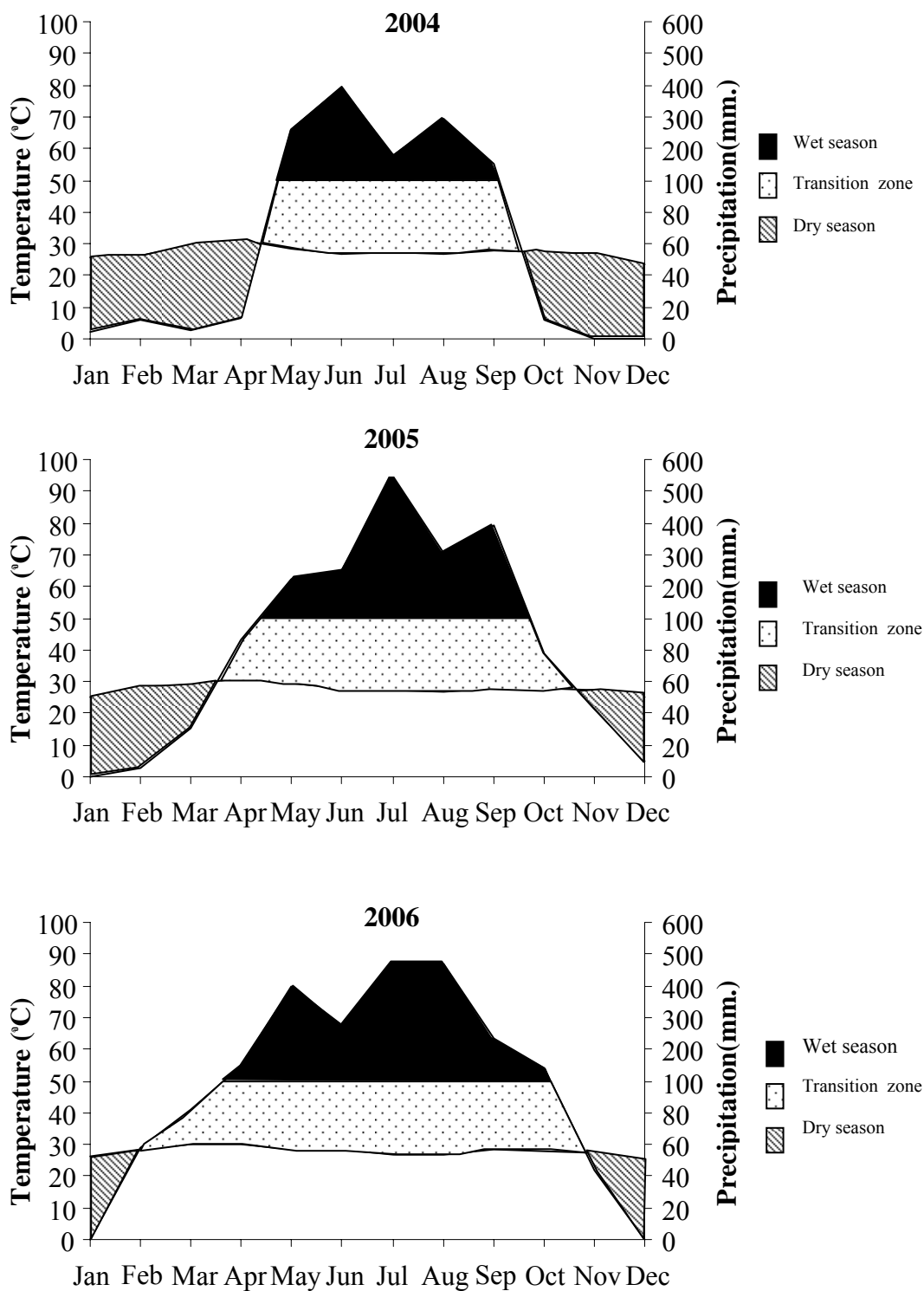
Appendix B Table 16 (Continued)

Scientific Name	Family	Thai Name
<i>Suregada multiflorum</i> (A. Juss.) Baill.	Euphobiaceae	Khan thong phayabat (ขันทองพยามาท)
<i>Syzygium claviflorum</i> (Roxb.) A.M. Cowan&Cowan	Myrtaceae	Wa hin (หว้าหิน)
<i>Syzygium siamense</i> (Craib.) Chanter. & J. Parn.	Myrtaceae	Chomphu nam (ชมพุน้ำ)
<i>Tectona grandis</i> L.f.	Lamiaceae	Sak (สัก)
<i>Terminalia alata</i> Heyne ex Roth	Combretaceae	Rok fa (รอกฟ้า)
<i>Terminalia bellirica</i> (Gaerth.) Roxb.	Combretaceae	Samo phi phak (สมอพิเภก)
<i>Terminalia triptera</i> Stapf	Meliaceae	Khi ai (ขี้อาย)
<i>Toona ciliata</i> M. Roem.	Meliaceae	Yom hom (ยมหอม)
<i>Trema orientalis</i> (L.) Blume	Ulamaceae	Phang rae yai (พังแหรใหญ่)
<i>Trewia nudiflora</i> L.	Euphorbiaceae	Ma fo (มะไฟ)
<i>Turpinia pomifera</i> (Roxb.) DC.	Staphyleaceae	Makok phran (มะกอกพราน)
<i>Vernonia volkameriifolia</i> Wall.ex DC.	Asteraceae	Ya kae (ยาแก้)
<i>Vitex peduncularis</i> Wall. Ex Schauer	Lamiaceae	Ka sam pik (กาสามปีก)
<i>Wendlandia tinctoria</i> (Roxb.) DC.	Rubiaceae	Khaeng kwang (แข้งกวาง)
<i>Wrightia arborea</i> (Dennst.) Mabb.	Apocynaceae	Mok man (โมกมัน)
<i>Xerospermum noronhianum</i> (Blume) Blume	Sapindaceae	Kho laen (คอแลน)
<i>Xylia xylocarpa</i> var. <i>keri</i> (Craib&Hutch.) I.C. Nielsen	Mimosaceae	Daeng (แดง)
<i>Ziziphus rugosa</i> Lam.	Rhamnaceae	Ma khwat (มะควัด)

APPENDIX C

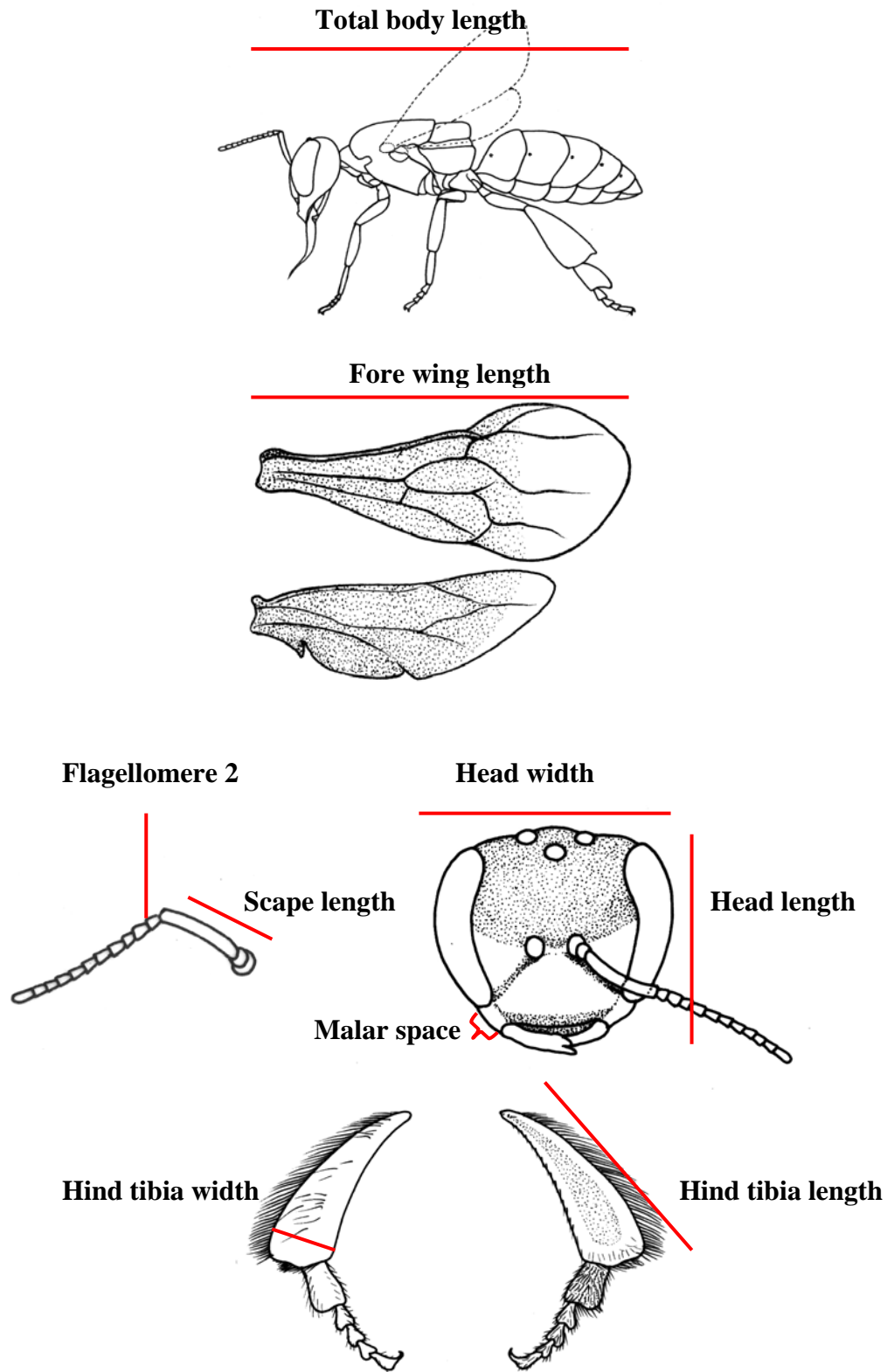


Appendix C Figure 1 Seasonal changes in air temperature, Relative Humidity and precipitation in four types of forest during April 2004 to March 2005 at Thong Pha Phum District, Kanchanaburi Province.

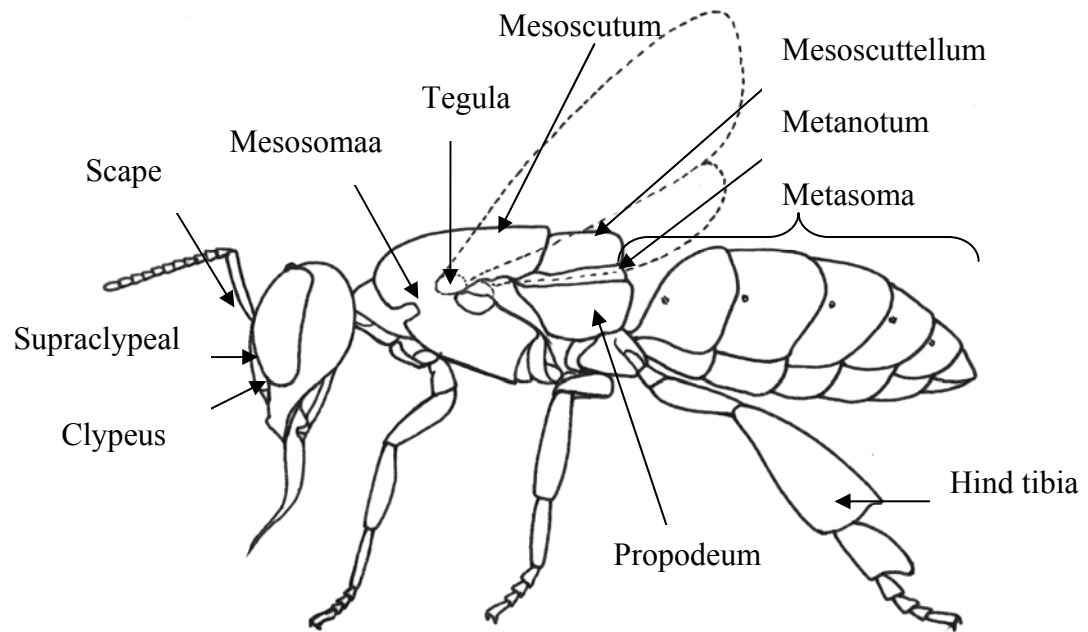


Appendix C Figure 2 Seasonal changes in air temperature and precipitation during April 2004 to March 2005 at Thong Pha Phum District, Kanchanaburi Province.

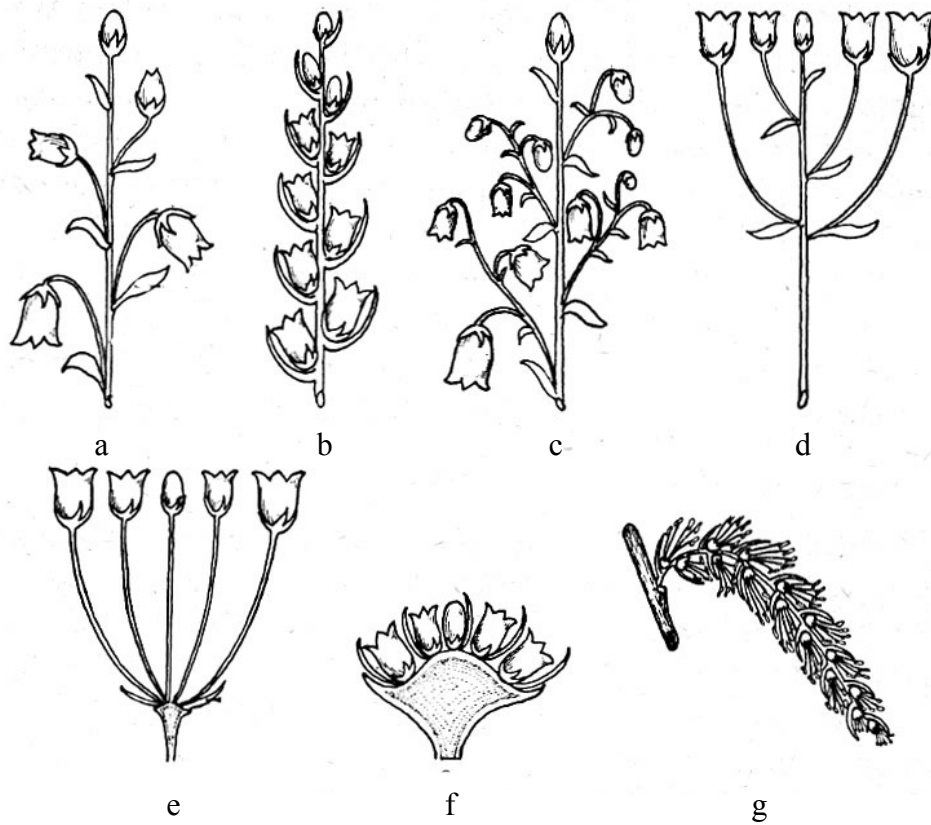
Source: The Meteorological Department.



Appendix C Figure 3 Stingless bee measurements.



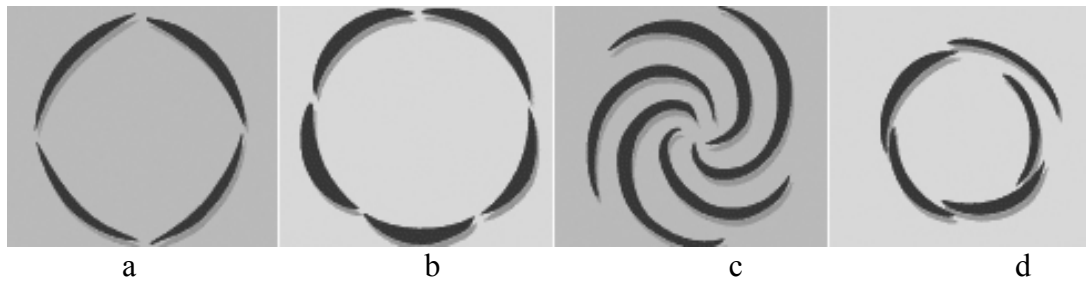
Appendix C Figure 4 Diagrammatic representation of a left lateral view of a stingless bee with major morphological features labeled.



Appendix C Figure 5 Type of inflorescence.

- | | | |
|-----------|----------|------------|
| a) raceme | b) spike | c) panicle |
| d) corymb | e) umbel | f) head |
| g) catkin | | |

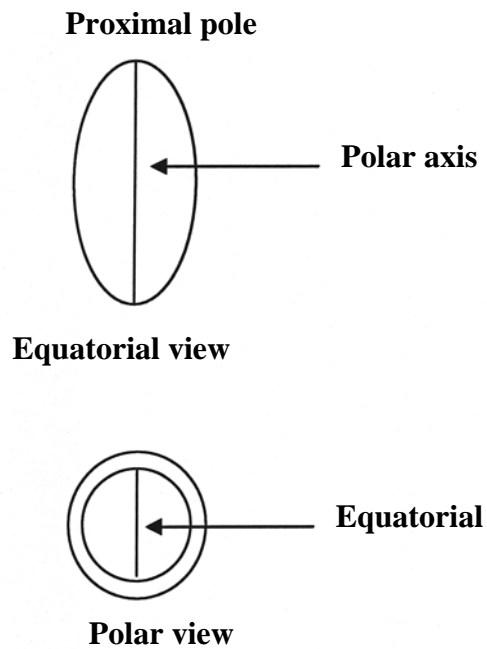
Source: modified from McMinn, H. E. and E. Maino (1951)



Appendix C Figure 6 Types of arrangement (aestivation) of sepals and petals in flower buds.

- a) open b) valvate
c) convolute d) imbricate

Source: modified from Anonymous (2008)



Appendix C Figure 7 Pollen measurements.

Source: modified from Dejtsakadi (2005)