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Diversity of Stingless Bees in Bamenda Afromontane Forests – Cameroon: Nest architecture, Behaviour and Labour calendar

Dissertation

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Dedication

To my parent who are of blessed memory:

Chui George Ntobukeu NJOYA and Tohjeuh Elizabeth Bah.

ABSTRACT

Until now almost nothing was known of invertebrates such as wild bees in the Bamenda highland forest region in Cameroon. This study focuses on honey producing bee species which do not possess functional stings. The diversity of the stingless bees in this area as well as their nest biology and behaviour was studied.

In all, Six species of stingless bees grouped into four genera exist in the Bamenda afro-montane forests. The four genera are: *Meliponula* (3 species), *Dactylurina* (1species), *Hypotrigona* (1 species) and *Liotrigona* (1species). The most represented of the species in Bamenda was *Liotrigona*.

Stingless bees were found to have huge variations in habitat preferences and in nest architectures. Nest designs differ with species as well as the habitats. Nest were found in tree trunks, mud walls, traditional hives, in soils or even just attached to tree branches. Brood cells and storage pots differ from species to species. Some species constructs combs while others construct cluster cells. Cell arrangement varied between horizontal and vertical doubled layered combs to clusters of cells.

Analysis of the behavior of stingless bees in an observation hive showed that the queen spends most part of her life on already provisioned cells. Workers clean the nest during the early hours of the day and dump the dirt just below the nest entrance. Workers were never seen laying trophic eggs. Bees are generally calm during manipulation. No case of attack on body parts was registered during the research period. The queen only become aggressive when disturbed from laying egg.

Results from study on division of labour among workers, showed that the lifespan of a workers of *M. becarri* range between 24- 73 days with an average longevity of 52.7days. Young workers 2 - 29 days were engaged nest construction. Workers starts foraging at the 25th day and last till they are 68 days old. The workers become guards after 55days. The most frequent tasks performed by surviving workers were: collection of resin (34.8%), construction of involucrum (33.3%), construction of pillar (31.1%) cerumen works (25.3%) and pollen collection (24.5%). Only 60% of surviving workers carried out foraging activities.

KURZFASSUNG

Über die Wirbellosenfauna im Bamenda Hochlandgebiet Kameruns ist bislang wenig bekannt. In der vorliegenden Arbeit wurden die Bienengemeinschaften dieser Lebensräume unter besonderer Berücksichtigung der Stachellosen Bienen untersucht. Neben der Erfassung der Artenvielfalt wurde hierbei die Biologie bestimmter Arten Stachelloser Bienen näher untersucht.

Insgesamt wurden 6 Arten von Stachellosen Bienen im Untersuchungsgebiet nachgewiesen, die sich auf 4 Gattungen verteilen: *Meliponula* (drei Arten), *Dactylurina* (eine Art), *Hypotrigona* (eine Art) und *Liotrigona* (eine Art). Die Anzahl nachgewiesener Nester deutet auf einen Rückgang Stachelloser Bienen im Untersuchungsgebiet innerhalb der letzten Jahrzehnte hin.

Die Nester der Stachellosen Bienen wurden in unterschiedlichen Habitaten gefunden. Die Anordnung der Brutzellen variierte zwischen horizontal und, vertikalen doppellagigen Waben bis zu clustern von Brutzellen. Außerden wurden unterschiedliche Formen bei den Nesteingängen gefunden.

Die Analyse des Verhaltens Stachelloser Bienen in den Kunstnestern zeigte, dass taglich Königin den größten Teil ihres Lebens zwischen den Brutwaben verbringt. Die Arbeiterinnen reinigen ihr Nest vor Beginn der Flugperiode und laden Abfälle unter dem Nest-Eingang ab. Arbeiterinnen wurden nicht bei der Eiablage beobachtet. Königinnen verhielten sich ausschließlich dann gegenüber Arbeiterinnen aggressiv, wenn sie von diesen während der Eiablage gestört wurden.

Ein Experiment, bei dem 90 Arbeiterinnen individuell markiert wurden zeigte, dass die Lebensspanne von *M. becarri* zwischen 24-73 Tage beträgt. Bei den Arbeiterinnen von *M. becarri* ist in den bestimmten Altersstadien eine gewisse Spezialisierung bei der Übernahme von Aufgaben, wie die Reinigung des Nestes und Wächteraufgaben, zu beobaditen. Ein Wechsel zwischen bestimmten Aufgaben wurde nur in wenigen Fällen beobachtet. Junge Bienen inAlter von 2-29 Tagen bauen am Involucrum und Brutzellen. In alter von 25-68 Tagen werden die Bienen zu Sammlerinnen. Nach dem 55 Tag übernehmen die Arbeiterinnen Wächterdienste an Nesteigang. Mit den folgenden Arbeiten waren die Bienen am meisten bescäftigt: Sammeln von Harz 34.8 %, Bau des Involucrums 33.3 %, Bau der Wabe (31.1 %) Bau des Cerumens (25.3 %) und Pollensammeln (24.5 %). Im Gegensatz zu anderen Arten Stachelloser Bienen betrug der Anteil des Nahrungssammelns bei Arbeiterinnen von *M. becarri* an dem Gesamtumfang durchgeführter Arbeiten nur mit bis zu 60 %.

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GENERAL INTRODUCTION

Stingless bees are a group of small- to medium-sized bees with vestigial (non functional) stings. They store honey and pollen and occur in perennial colonies. Stingless have attained the most advanced level of social organization which can only be comparable to that of honeybees (SAKAGAMI 1982). There are several hundred of species existing worldwide, which differ significantly in colour, body and colony size (ROUBIK 1992, MICHENER 2000). In Africa stingless are distributed throughout the tropical and subtropical parts where they occur sympatrically with the honeybees (KAJOBE, 2007). They are often stated as generalist flower visitors (visits many different flowers) and important pollinators of crops though with little or no review on this assertion.

1.1 Taxonomy and Phylogeny of Stingless bees

Stingless bees belong to the family Apidae and tribe Meliponini. The classification of stingless bees has been presented differently by different authors (SAKAGAMI 1982 review). WILLIE (1979) was the first to recognize common characters of the African Meliponini, regarding the African group as the ancestral and placing them into five genera. Meanwhile, CAMARGO & PEDRO (1992b) brought out the major division of African Meliponini genera and that of non Africa. African taxa show remarkable external similarities to that from the Americas (MICHENER 2007). The African *Dactylurina* resembles the *Trigona*; African *Plebeina* resembles *Plebeia*, *Liotrigona* resembles *Trigonisca* and African *Meliponula* resembles *Melipona*. The African genera and the several group of stingless bees from other continents appeared to exhibit parallel evolution with members of the groups haven acquired similar characteristics independently, though coming from related ancestral lineage. (WILLIE 1979).

1.2 Diversity and distribution of stingless bees

Stingless bees are monophyletic (halophyletic) groups which are principally found in tropical and subtropical areas of Americas, Africa, Australia, and parts of Asia (ROUBIK 1989). Meliponini extends up to 28°S - 35°S and 23.3°N. Unlike honeybees (Apis) with approximately 11 species in one genus, stingless bees consist of several hundred species distributed into 26 genera world wide (MICHENER 2000). The highest distribution of these bees is found in tropical

Americas. EARDLEY (2004) indicated that there are 19 existing species grouped into 6genera which are currently documented in Africa. The six Africa genera are: *Cleptotrigona*, *Liotrigona*, *Hypotrigona*, *Dactylurina*, *Meliponula* and *Plebeina*. The exact number of species of stingless bees in Africa is not yet known because of the gaps in research in this field of study in Africa.

1.3 Differences between honeybees (*Apis*) and stingless bees (Meliponini)

Honeybees and stingless bees share many similar characteristics, notably in the honey production and in their social life style. These characters sometimes make it difficult for some people to be able to differentiate between the honey bees and stingless bees. However, the stingless bees can easily be distinguished from the honeybees by the following main morphological and behavioral characteristics below:

1. Generally, the stingless bees are smaller in size than the honeybees
2. Stingless bees honey is more liquid than the well known honey bee honey
3. Stingless bee do not possess function stings and so do not sting
4. The males of stingless bees do not have a membranous endophallus (undifferentiated sexual tissues in insects) while the males of honey bees possess this structure (OTIS 1997).
5. The pattern of wing venation is reduced in stingless bees, but stretches in honeybees.
6. Stingless bees have many more species (374spp) than honey bees with fewer species (11spp)
7. The stingless bees do not have effective thermo-regulation properties as the in honeybees but they use the involucrum surrounding the brood s to maintain nest temperature above ambient temperature; however, no temperature homeostasis has been found. (RUTTNER, 1988)

1.4 Importance of stingless bees

Stingless bees can play an ecological role as pollinators of wild plants since they are polylectic.
They are ideal for comparative studies because of the large variety in the biological and ecological features they possess.

Stingless bees can also play an economic role both as cash crop pollinators and from the honey the bees produce. The medicinal properties of stingless bees honey and propolis, can greatly impact human health.

1.5 Reproduction in stingless bees

As in all insects that undergo complete metamorphosis, each bee passes from the egg, to the larva, the pupa before attending the adult stage. The fertilized eggs of the bees develop into females whilst the unfertilized eggs develop into males. When the queen mates, she stores sperm cells in her spermatheca. She normally receives a lifetime sperm cells supply. She can then control the sex of each egg by liberating sperm cells from the spermatheca as the egg passes through the oviduct.

There are two ways of reproduction in social insects: either by increase in the number of individuals (colony development) which depends mainly on the egg laying ability of the queens. The number of eggs laid per day varies among species and does not change much with the variation in seasons as is the case of honeybee species. Another mode of reproduction is by simply increasing the number of colony (colony reproduction) whereby a new colony is created by reproductive swarming. In the case of stingless bees the young virgin queen moves out with the swarm but maintains the connection between the daughter nest and mother nest which can last for weeks or month (KAZUHIRO et al. 1999).

1.6 Brood organization, cells arrangement and oviposition in stingless bees

There are three different possible ways by which stingless bees can construct cells. These three types of cell constructions are described in the schema below. Schema and terminology are modifications from SAKAGAMI (1982).

Each schema shows that there are two successive oviposition processes, each having four cells represented schematically by the gradual growth of the cells. S = start of cell construction; C = completed cells (collard cells); O = Oviposited cell.

1. **Successive type (S_c) of cell construction:** Building of cells starts anytime so that various growth stages of the cells are found at a given time. No half cells are found soon before and after the oviposition process (Fig. 1.)

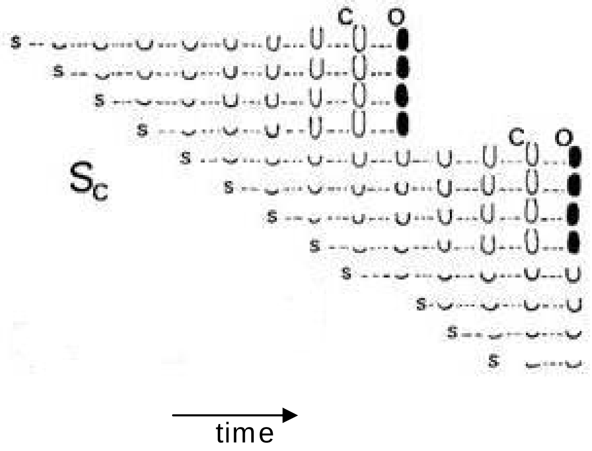


Figure 1. Schema showing successive (S_c) type of cell construction

2. **Synchronous type (S_y):** All cells are almost started at same time usually shortly after the last oviposition and only cells of similar growth stages are found at any given time.

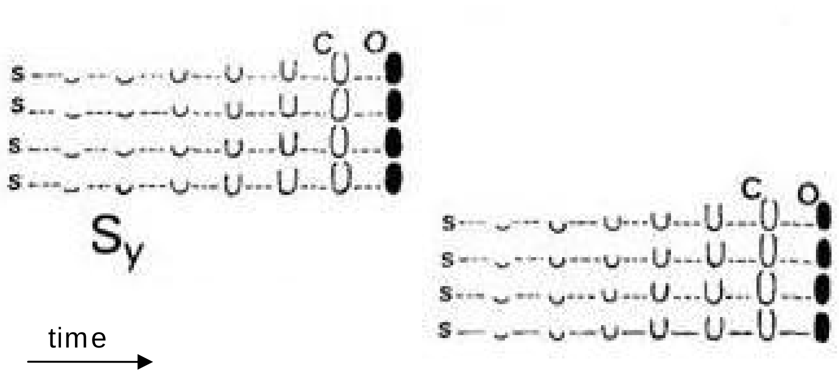


Figure 2. Schema showing synchronous (S_y) type of cell construction

3. **Semisynchronous type (S_m):** Cell building start successively but the different in the growth stages becomes gradually smaller. No half built cells are found soon before or after the oviposition process. The start of new cells is delayed once the cells under construction attained an advance stage.

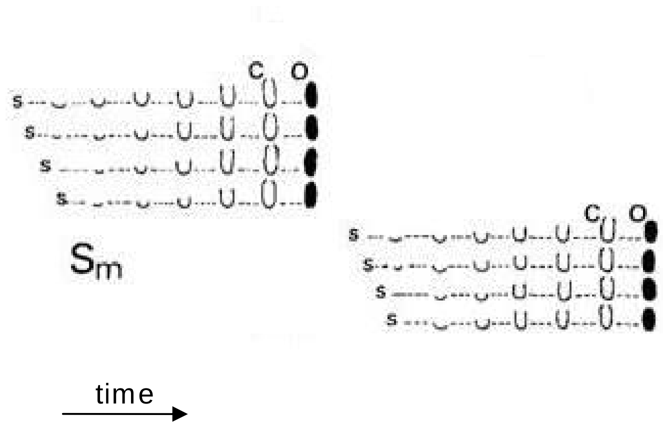


Figure 3. Schema depicting Semisynchronous (S_m) type of cell construction

The mode of queen oviposition (egg laying) into individual cells in stingless bees can also be categorized into three main categories as seen from the schema below;

1. **Exclusively batched (B_e) oviposition:** The queen always lays her eggs into a group of cells within a short time. The number of ells per batch as wells as the interval between batches is relatively large and stable.

Figure.4. Exclusively batched formation in stingless bees under hypothetical colony conditions

2. **Facultative batched (B_f) oviposition:** Oviposition is loosely batched. The number of cells per batch and the interval between batches varies and sometimes ending in singular oviposition.

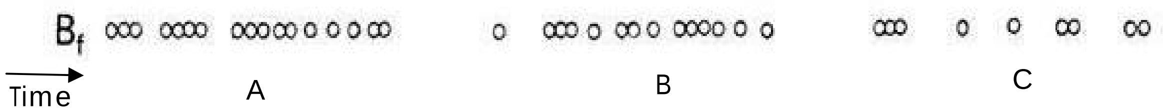


Figure.5. Facultaively batched formation in stingless bees under hypothetical colony conditions

3. **Predominantly singular (B_s) oviposition:** Each oviposition is usually separated by sufficiently long interval, though occasionally two or more oviposition forming a batch.

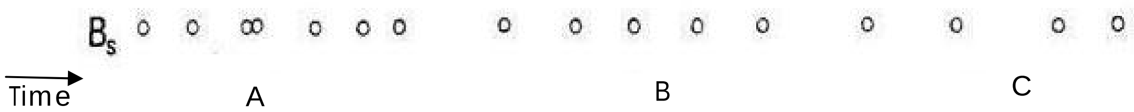


Fig.6. Predominantly Singular formation in stingless bees under hypothetical colony conditions

N.B. A = Favorable conditions, B = Intermediate conditions, C = Unfavorable conditions

1.7 Temporal sequences of Provisioning and Oviposition Process (POP)

Focusing on a queenright stingless bee colony the daily rhythms can show the following divisions; the Quiescent (Q), Transient (T), and Oviposition (Ō) periods. The sequence is clear in the taxa that exhibits synchronous exclusively batched type (S_yB_e) of cell construction and oviposition, but it becomes less distinct in other taxa, especially when many collared cells (cells ready to be food provisioned) occur anytime as in Mourella (WITTMANN et al. 1991). The oviposition period (Ō) can be divided into 3 main subphases:

1. Patrolling phase (P): from the first visit by the queen to the brood cell area after the quiescent phase the start of the next stage
2. Arousal phase (Ā), from the final visit by the queen to the brood cell area to the start of the next stage(Ō);
3. Oviposition phase (Ō), from the queen final arrival at one of collard cells to the completion of the operculation of the last oviposited cell of a batch).

During the patrolling phase the queen may leave the brood cell area frequently or not. In some taxa, once the queen arrives at the brood cell area, she may cruise on the area (C) or wait (W) by particular cells.

The Oviposition stage of each batch is also temporally and sequentially arranged. In taxa whose cells are successively provisioned (Fig 1, S_c) the sequence becomes:

$\overline{P}_1$ - Predischarge phase, from the queen´s arrival at the first cell to the start of food discharge,

$\overline{d}_1$ - Food discharge phase, from the first food discharge by a worker into a cell to the start of oviposition;

$\bar{O}_1$ - Queen Oviposition, from cell inspection by the queen to completion of oviposition and

$\overline{S}_1$ - Operculation phase, from the queen´s withdrawal from the cell to completion of cell sealing.

The same sequence is repeated for the second and subsequent cells ($\bar{u}_2$ ... $\bar{u}_1$ … $\bar{u}_{n..}$ as .. $\overline{r}_i$, $d_{i,}$ $\overline{o}_{i,}$, $\overline{s}_i$). (see Fig.1,2&3)

Summarizing, the daily life of a colony gives $\overline{Q}$ + $\overline{T}$ + $\overline{O}$; Period

$\bar{O} = \overline{P} + \bar{A} + \bar{O}$ stages; stage $\bar{O} = \overline{r}\ r_i + d_{i,} + \overline{o}_{I,} + \overline{s}_i$ Subphases

In the taxa in which provisioning occurs synchronously in several cells with high agitation (as in Mourella), the sequence; $\overline{r}_{I,}$ $d_{i,}$ $\overline{o}_{i,}$ can differ among cells (Fig 1) and $\overline{r}_1$ is not always followed by $\overline{d}_1$.

Cell operculation phase ($\overline{s}$ = sealing of oviposited cell) of stingless bees consist of 4 sub phases (WITTMANN et al. 1991):

1. Preoperculation ($\overline{S}_p$) = from the end of oviposition $\bar{O}$ to the start of rotation by worker that closes the cell
2. Main rotation ($\overline{S}_r$) = from the end of $\overline{S}_p$ to the first withdrawal of the metasoma tip from the cell
3. Transient ($\overline{S}_t$) = from the end of $\overline{S}_p$ to the final appearance of rotation and
4. Side work ($\overline{S}_s$) = from the end of $\overline{S}_t$ to the disappearance of cell opening.

1.8 Division of labor among workers of stingless bees

The social life of stingless bees can be characterized by two kind of division of labor: Division of castes (reproductive system) and division of labor among workers (productive system). The females of stingless bees are divided into two castes: queens and workers. Queens are much larger than the workers and lack corbiculae and wax glands. As workers grow older, their tasks changes. The sequence of activities can be divided into stages.

1.9 Communication and foraging

Stingless bees are able to communicate the location of a food source to their nest mates. Some use chemical scents secreted from their mandibular glands and position of the sun for orientation. Foraging workers stop at intervals of certain distance and leave scent trays on the way from a good source of food to the colony. Others leave the nest and follow the odours outward while others will guide nest mates to a good food source by leading the way for the others in a group or individually back and forth for several trips. Some will communicate with sounds and zigzag running (KAZUHIRO et al. 1999). Stingless bees can forage without the help of ultraviolet light. Most stingless bees are polylectic, foraging a wide range of crops for pollen.

1.10 Research Goals

The central focus of this research is to find out the diversity of species of stingless bees found in the Bamenda Afromontane forests and provides information of their nest architecture and behavior. The design of this research is based on the overwhelming lack of knowledge of these bees in the area of research.

1.10.1 Research questions

- Are there as many genera of stingless bees in the Bamenda highlands as in Africa?
- How and where do these bees design and construct their nests?
- How do these bees ensure development of colony or increase in the number of individuals in the colony?
- How often are the young bees reproduced?
- Which bees are involved in the tasks of maintaining survival of the colony and in reconstruction of the nest?

1.10.2 Specific objectives

- Find out the different species of stingless bees in the Bamenda afromontane forests.
- Find out the distribution of the different species in the area
- Study the nest biology and habitat preferences of the different species of stingless bees in the Bamenda afromontane forests
- Investigate food provisioning and eventual oviposition in *Hypotrigona gribodoi*
- Investigate the pattern of tasks allocation by the workers of *Meliplebeia ogouensi* in the colony

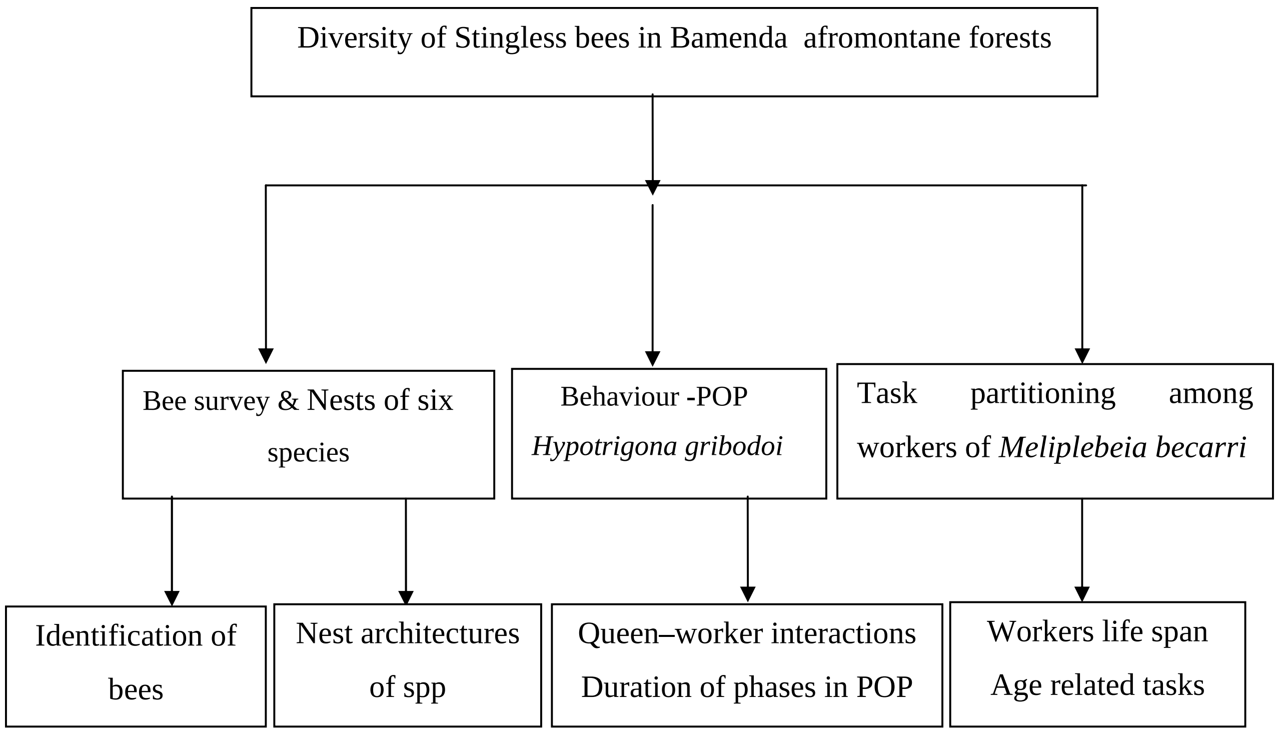


Figure 7. Sketch summary of research question and specific objectives

1.11 Study area

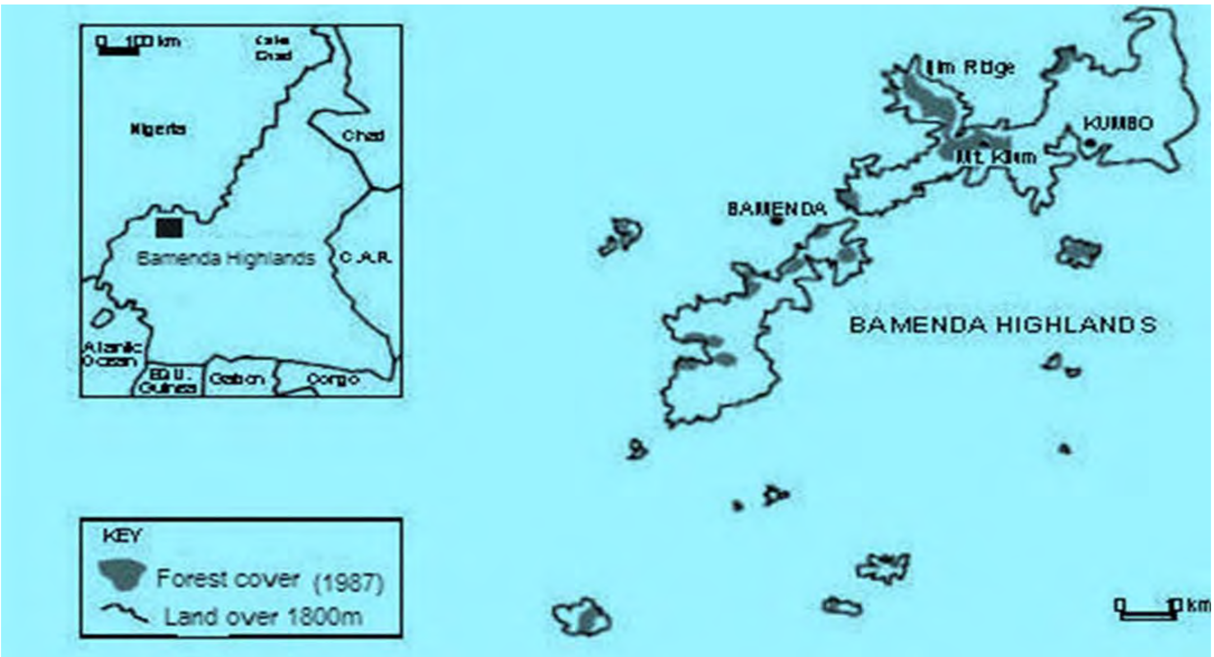


Figure 8. Location of Bamenda highlands and approximate distribution of forests

1.11.1 Why Bamenda Highlands?

The Bamenda Highlands are part of a chain of Mountains known as the Cameroon Mountains with a surface area of more than 20,000 km^2. This area supports the last remaining extensive patches of Afromontane forests in West and Central Africa with high level of endemism. The montane forests are collectively considered as a priority for conservation on a global scale. The forest patches in the region are of varying degrees of biological, socio-economic and cultural significance to the densely populated adjacent communities. FISHPOOL & EVANS (2001) cited seven bird species of global conservation concern, five of which are globally threatened. The Mount Oku region harbours six endemic mammals (HUTTERER & FULLING 1990) and holds viable populations of endangered or vulnerable primates.

Destructive human activities in this region include, the rearing of domestic animals that prevents natural regeneration, the spread of uncontrolled bush fire, hunting, the clearance of bushes for farms within the forest, large scale collection of firewood, the over cutting of trees for carving and commercial bark striping particularly in the case of medicinal tree *Prunus africana*. This unsustainable use of the forest inevitably leads to habitat alteration and fragmentation, which can lead to species extinction.

Considering on-going threats to the biodiversity in the region there are concerns that many of the plants and wildlife species may completely disappear even before they are known.

As an endangered ecosystem and an ecological area of unique biodiversity, it therefore offers a very high scientific value. This area has been earmarked for the establishment of an extensive conservation network aimed at conserving the unique flora and fauna of the area.

Virtually nothing is currently known about the stingless bees, their habitats and the process of oviposition in this area.

1.11.2 Vegetation and Relief

The topography of the area varies greatly from 400m in the lower depressions to over 3000m above see levels on the mountains. Topography can be characterized into 3 categories: the lower altitudes (<900m), mid altitudes 900-1500m) and higher attitudes (>1500m). The grassland vegetation covers the high altitudes zones and the lower and mid altitudes are characterized by savanna cover with wood and shrubs. The area is composed of many types of soils; Loamy –clay in the high altitudes to sandy-loam in mid altitudes and to lateralitic soils in the valleys.

1.11.3 Climate

The climate of this area is highly influenced by the relief and topography. The montane areas are cold with temperatures below 15°c whereas the lower attitude areas are hot with average temperature of 27°c. Generally, the climate is describe as the tropical transitional type in the main mountainous regions in Cameroon with rainy, humid and continuous warm climate in the south and to the highly diverse but relatively dry and hot climate to the North. There are basically, two main seasons in this area; the rainy season which starts from mid March to Mid October, and the dry season period between Mid October and Mid March. Annual rainfall varies considerably from 1300mm in the low attitudes to over 3000mm on the highest mountain area

2 DISTRIBUTION OF STINGLESS BEES IN THE BAMENDA HIGLANDS

2.1 Abstract

The Bamenda highland afromontane forest region habours a total of six stingless bee species grouped into four genera. The four genera are: *Meliponula* (3 species), *Dactylurina* (1sp), *Hypotrigona*(1sp) and *Liotrigona*(1sp). Of the six species present in this region, *Meliplebeia becarri* was found to be the only subterranean species and *Dactylurina staudingeri* the only species that construct complete exposed nests attached on the branches of fruit trees. The other four species constructs their nests either in tree trunk cavities, in abandoned honey bee hives or on mud walls. Meliponiculture is still very poorly developed in this region as well as in other parts of Cameroon. Generally, the number of existing colonies of stingless bees in this area appears to be on decline. Due to recent scarcity in the number of colonies of the stingless bees colonies, fewer people are interested in meliponiculture nowadays compared to years ago. Harvesting of stingless bee honey is still done using very primitive methods which results in destruction of the nests, killing of the brood and spilling of honey. Though stingless bees are not as productive as honey bees in terms of honey quantity, meliponiculture could help in poverty alleviation in the rural areas if developed and practice in large scale as is the case with apiculture.

2.2 Materials and methods

A preliminary survey of bees was carried out in 2007, during which time stingless bees where collected wherever they were found in the region. The potential nesting sites of stingless bees were identified and documented. Representative sample of each species already collected was mounted into a small portable collection box (10 cm^2). The sample collection was used as a guide to ease understanding and recognition of stingless bees when talking to rural people in the various communities. The sample collection was presented to local farmers, hunters and beekeepers that assisted in locating nesting sites of other stingless bees' species and new colonies. Nests were found both by chance and from information provided by the hunters, farmers and beekeepers. This was repeated in all of the areas we visited for data collection. Nests were located from the information provided by the beekeepers and hunters. Information provided by these informants on the availability and number of colonies was registered. Besides the data collected through the show and tell semi structured method, personal interviews during field trips were also used.

The different nest locations, GPS coordinates, number of colonies as well as the local names of the stingless bees were registered. Samples from the collection were sent to two renowned stingless bee taxonomists: David W. Roubik (Smithsonian Tropical Research Institute, Panama) and JMF Camargo (University of Sao Pauölo, Brazil) for proper identification.

2.3 RESULTS

2.3.1 Identification of bees

Table 1. Stingless bees found in thy study area (identified by David Roubik and Camargo)

ID per David W. Roubik Scientific names	**ID per JMF Carmago** Scientific names	**Nesting sites**	**Local names**
Meliponula becarri	*Meliponula ogouensis*	Subterranean	nwauah
Dactylurina staudingeri	*Dactylurina staudingeri*	Tree branches	
Meliponula bocandei	*M. bocandei*	Tree trunk Traditional hives	
Hypotrigona gribodoi	*Hypotrigona gribodoi*	Tree cavity on branches	
Liotrigona bettogoi		Mud walls Bamboos crevices	
Meliponula ferruginea	*Meliponula ferruginea*	Traditional hives Tree trunks	

The genus names of five species of the stingless bees were identified by the two taxonomists found to be same. However, the species name for *Meliplebeia* was found to be different as seen in table 2.3.1 above. More confirmation is required for the species.

2.3.2 Abundance and distribution of stingless bees in Bamenda highlands

Table 2. Location and number of colonies of stingless found in the Bamenda highlands.
+ implies that the actually number of existing colonies could be more, given that only the most reliable information gathered from informants were registered.

For the GPS coordinates of the existing colonies of stingless bees in the region, see the distribution map below and in appendix.

Scientific names	**Locations found (villages)**	**Number of colonies found**
Meliplebeia becarri	Takijah	11
Dactylurina staudingeri	Lip, Maboua	6
Axestotrigona ferruginea	NduMbasang Lip Saranka	4
Meliponula bocandei	Lip Maboua	4
Hypotrigona gribodoi	Dom Maboua	2
Liotrigona bottegoi	Lip Ndu Dom Chaw Maboua	20+

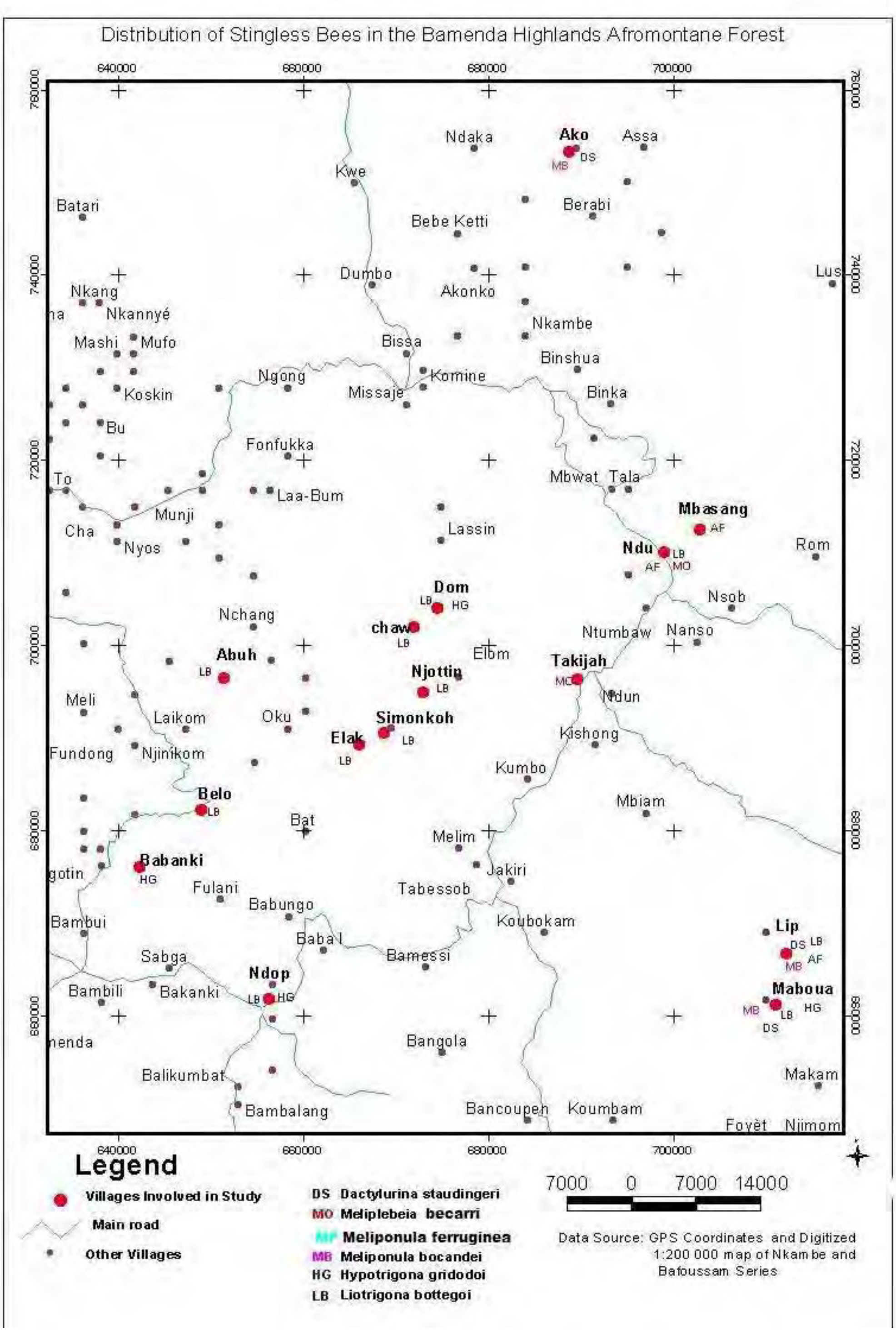


Figure 9. Map showing the distribution of stingless bees in the Bamenda highland forests

2.4 Conclusion

Among the six species of stingless bees present in the region, *Meliponula ferruginea* and *Meliplebeia becarri* appeared to be the most widely used species by the local people. These bees are used mainly for honey production. Few individuals keep these bees for the purpose of honey production. However, most of the stingless bee honey used by the local people came from wild colonies. *Meliplebia becarri* is the second most abundant of all the stingless bees (Meliponine) found in the highlands after *Liotrigona bottegoi.* So far colonies of *M. becarri* was only registered around Takjah village.

Meliponiculture which use to be widely practice in the Bamenda highlands appears to be declining because stingless bees colonies are becoming more difficult to find. The likely cause of the decline in the number of colonies is the destruction of their habitats and nesting site. Also, the destructive manner of harvesting the honey contributes to the disappearance of colonies.

3 NEST ARCHITECTURE OF SIX SPECIES OF STINGLESS BEES IN BAMENDA HIGHLANDS OF CAMEROON

3.1 General summary

The architecture of six species of stingless bees in Cameroon reveals considerable designs in their brood cell arrangements, storage pot arrangements, nest entrance shapes and nest construction. They nest in ground, in tree trunk cavities, mud walls of houses and in abandoned honey bee hives. Brood cells are arranged either in vertical combs, horizontal combs or in clusters. Cells vary in sizes and shapes and the brood area is either protected with involucrum or not. Some nests are protected with batumen sheets while others do not have this protective sheet.

3.2 INTRODUCTION

Stingless bees are known to be generalists with regards to selection of nesting sites (HUBBELL & JOHSON, 1977; ROUBIK, 1989). Their nests in felled trees, in bush that has been burnt or that has been trampled or cut by man or other animals, in the earthen banks of road cuts, paths, field, and in banks made by rushing water, have often provided the opportunities to study bee nesting biology (MICHENER 1974; ROUBIK 1989).

The several hundreds of stingless bee species existing worldwide differ considerably in colony size, in body size and colour (DRUMOND et al. 1997; MICHENER 2000). These bees also vary considerably in their nest architecture with different designs in brood cells arrangements. Brood cells are arranged in horizontal or vertical combs, semi combs or in clustered cells. The nests can either be constructed in crevices, in trees or in the ground (WILLE & MICHENER, 1973; ROUBIK, 2006).

SAKAGAMI (1990), noted that the elaboration of their nest entrance is generally species specific. KAJOBE & ROUBIK (2006), affirms that attributes of the nests are useful in taxonomic studies especially in equatorial tropical Africa where little has been studied.

Some previous studies on nest biology of stingless bees have been carried out by SAKAGAMI (1982); ROUBIK (2006); ELTZ et al.(2002, 2003); SLAA (2003); KAJOBE & ROUBIK (2006).

Stingless bees have evolved adaptive nest constructions strategies which have resulted in sophisticated nest architecture in many species while others lack certain structural components (SCHWARZ 1948; NOUGUEIRA-NETO & SAKAGAMI, 1966; KERR et al., 1967; FONSECA et al.,

1972; WILLE & MICHENER 1973; CAMARGO 1970, 1974, 1980; ROUBIK 1979, 1983; CAMARGO & WITTMANN 1989).

Many species, particularly those of the moist tropics, are unable to withstand chilling temperatures (MICHENER 1974). One major component of the nests of stingless bees is the excellent insulation especially with the exposed nests. Nests in large trunks or in soils are particularly well insulated.

ROUBIK (1983) observed that the nests of many stingless bee species are yet to be described. This observation is especially important for equatorial Africa where very little studies have been done on stingless bees. In Cameroon, no previous studies on stingless bees, their nests or other related aspects has been done. This study therefore will constitute a description of nest architecture of some of the stingless bee species found in Cameroon and will provide more inside information on some of the species already studied else where

3.3 Materials and methods

These nests were excavated where necessary for the study of the nest architecture. The number of nests to be excavated depended on the available number of colonies of each species found in the field. A total of 25 nests were studied and their data used for the description of the nests. Measurements were focused on the following structures; Nest entrance, brood area, storage pots, involucrum layers, batumen sheets, size of cells, size of nest cavity and drainage tube for ground nesting species. Measurements were done using a ruler.

3.4 Nest architecture of *MELIPLEBEIA BECARRI*

3.4.1 Abstract

Meliplebia becarri is the second the most abundant of all stingless bees (Meliponine) found in the western highlands in Cameroon after *Liotrigona bottegoi*. These bees appear to be the most restricted range species of all the other stingless bees' species known in the western highlands of Cameroon. *M. becarri* was recorded from just one village area (Takijah) in the whole of the research area. The bees prefer to nest in Eucalyptus plantations and open farm lands with numerous lateral roots to be used as anchor for their nests. It is unknown whether these bees construct the cavities in which they fix their nests themselves or used already existed cavities of some animals to fix their nests. *M. becarri* always cohabits with small white ants and some little beetles. The nests of *M. becarri* are built in the soils and exhibits architectural characters which are typical to all other genera of obligatory ground nesting bees in Africa like Plebeiella and Plebeina. In *M. becarri* however, the nest proper consists of a brood area, area of involucrum layers, and storage pots area. The combs are horizontal and the mode of building comb is concentric while cell construction is synchronous.

The nests are connected to the exterior by a short outer entrance of 0.5-0.6cm above the soil and <0.1cm thick wall. A drainage of excess moisture measured 16.5cm long and 0.7-1.2cm diameter was observed below the nests cavity.

3.4.2 Nesting sites

A total of 11 nests of *M. becarri* were found in Takijah, Bui Division North West province of Cameroon. During the study period this species nests was only found in the Takijah village area and no where else in the Bamenda highlands. Nine of the nests were found in Eucalyptus plantation farms and two in open farmlands. Reports gathered from local people and bee keepers in the area, indicated that there could be as many as 25 colonies in the village area. Reliable sources (farmers involved in meliponiculture) also lamented that colonies of *M. becarre* are more difficult to find nowadays compared to some 10 years ago.

Figure 10: Nest site of *Meliplebeia becarri* in a tomato farm
(Notice the nest entrance surrounded by small pegs for easy location-arrow).

Figure 11: Nest site of *M. becarri* in Eucalyptus plantation
(Notice the nest entrance surrounded by small pegs to ease location of spot)

3.4.3 Nest cavity

The nests of *M. becarri* are constructed in open farm areas or in secondary forests with very scanty undergrowth and less dense canopy trees which allows ample light to reach the forest floor. These bees usually prefer soils with moderate size roots which they can use to anchor their nests. We did not find any reason to suggest that these bees take advantage of existing cavities of other social insects like ants or termites to build their nests.

The ceiling and the inner walls of the soil are hardened and smoothed by the bees so that the nest cavity can easily be separated from the surrounding soil. The entire nests fitted to the shape and size of the cavity, supported by protruding secondary roots passing through the nest, and the batumen lamellae and the pillars spanning the gap between the batumen layer and the cavity wall.

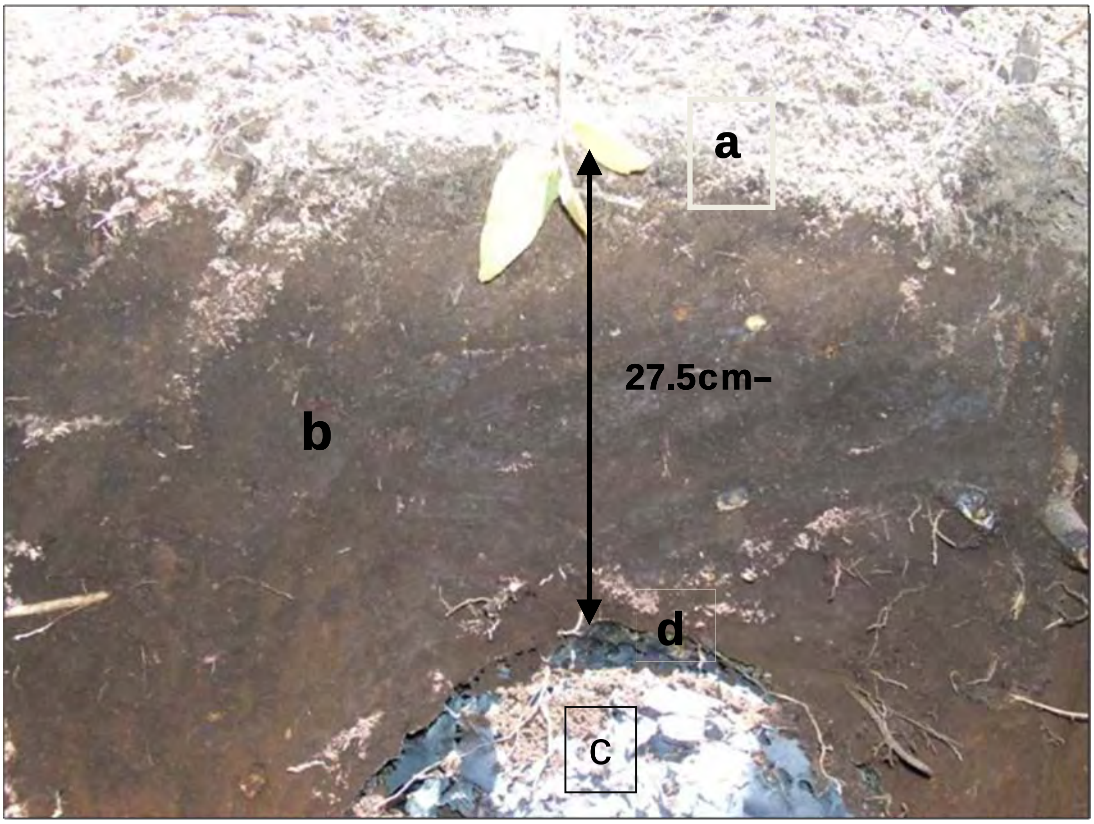


Figure 12. Excavation of subterranean nest of *Meliplebeia becarri* revealing the depth of the nest under ground: **a** = top soil layer, **b** = underground soil layer - B-horizon, **c** = nest cavity, . **d**=ceiling

3.4.4 Nest entrance

This subterranean species provides just a single entrance into their nest cavity. The nest entrance is usually hidden under dry leaves and grasses (Fig. 15 & 16). The external entrance tubes studied were 5 - 6 mm high with 1 – 2mm thick walls and always projects upward directly above the under ground nest. The external tube diameter was more or less the same in size to the diameter of the tunnel leading to the nest.

Figure 13. Nest entrance (external tube; arrow pointing to wall of external tube)

Figure 14. Nest entrance with guard bees

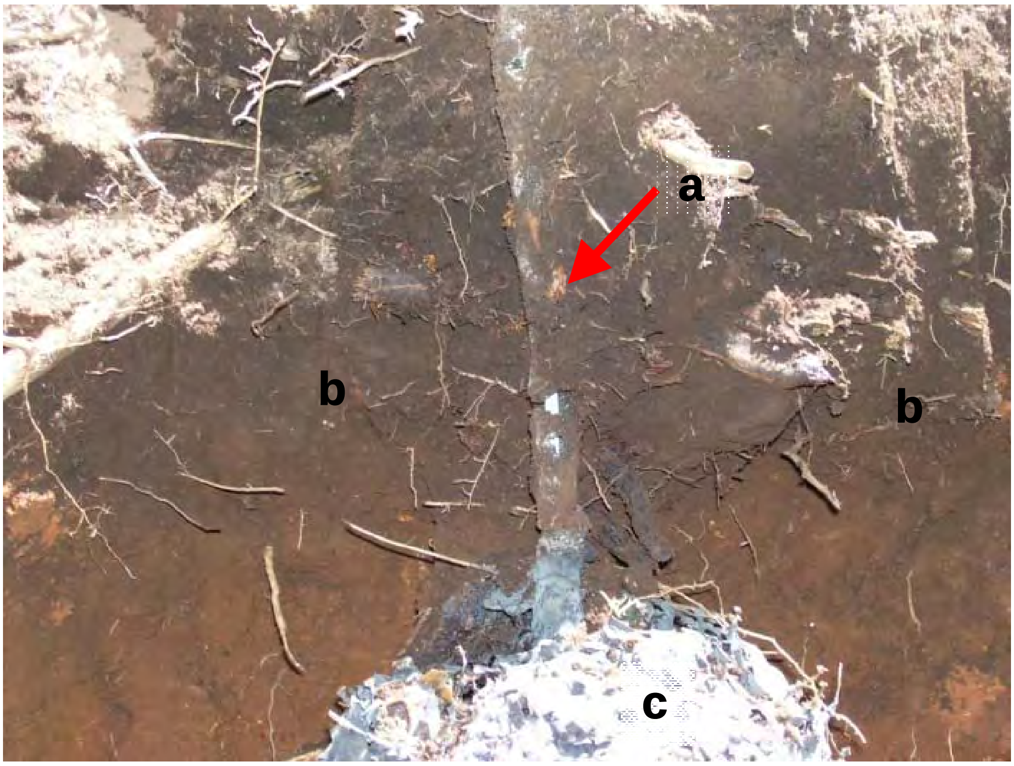


Figure 15. **a** = external nest entrance tube, **b** = soil horizon, **c** = nest cavity

3.4.5 Batumen layer and involucrum sheets

The nest of *M. becarri* is enclosed by a black and brittle 2-3 layers batumen. The batumen or external involucrum is about 1mm thick from which short pillars that protrudes to the unlined walls of the cavity. The nest cavities are 14-16cm high and 12-13cm in diameter. The shape of the nests could be oval or roughly rounded and flattened at the bottom.

At the lower part of nest, the batumen layer is partly opened by horizontal slits so that the basal layers of the involucrum and the storage pots are in direct contact with the substrate. The involucrum is attached to the batumen by tiny pillars. The brood chamber is surrounded by 6-8 layers of involucrum each measuring less that 0.5cm thick. The involucrum is made up of very sticky substances containing propolis, resin and sometimes plant materials. The involucrum sheets are brown and shiny and arranged in alternating layers that allows bees to move in between the layers and to the brood area.

Figure 16. Exposed nest showing outer and inner sheets of batumen (arrows)

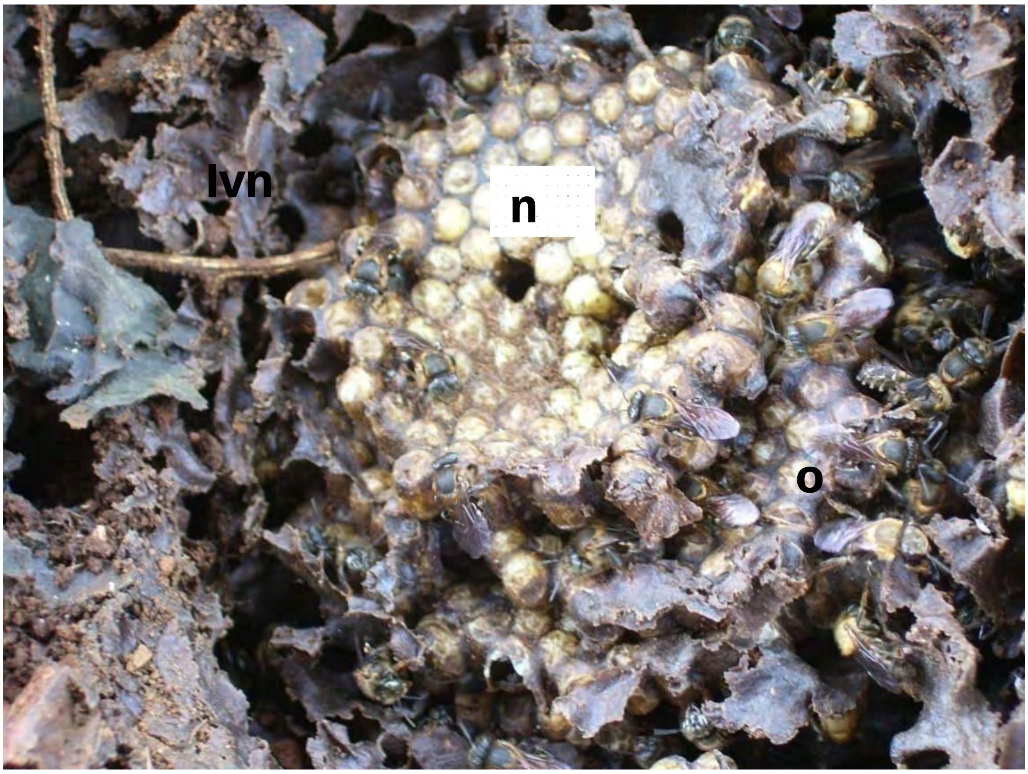


Figure 17. Involucrum and combs: Inv= involucrum, n=new comb cells, o=older cells

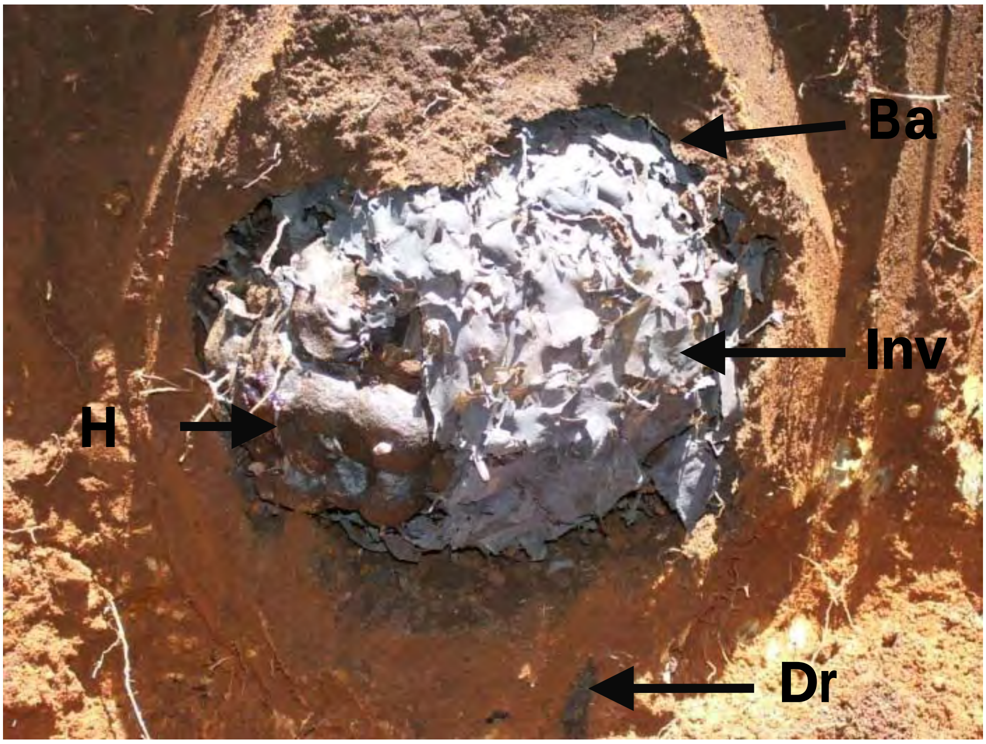


Figure 18. Nest showing most of the external features as seen underneath the soil surface **Ba** = Batumen, **Inv** = Involucrum, **Hp** =honey pot, **Dr** = drainage tube

Figure 19. Structure revealing pillars attaching honey pots to ceiling (arrow)

3.4.6 Brood area

The brood area is surrounded with sticky soft 6 - 8 sheets or layers of involucrum. The brood combs are horizontally arranged though they may appear concave at some points. The mode of construction of combs is concentric, that is, each comb is constructed from the centre outward towards the peripheries of the comb. Combs are firmly connected to one another or with involucrum by means of tiny pillars of about 2mm length. The area with old cerumen is immediately below the old brood comb and of the same diameter. Brood cells are cover with wax. The older cells and combs are found below while the newly constructed cells are above as shown in fig. 18.

Figure 20. Horizontal combs with each layer separated by pillars

Figure 21. Gyne cell at the edge of comb

Figure 22. Heart shaped comb with gyne cell

3.4.7 Storage pots

The pollen and honey pots cover the lateral part of the brood area. Each pot is on an average of 3-4cm high and 2.5 to 3.2 cm in diameter. Pollen pots are placed closer to the brood area than the honey pots. The pollen and honey pots are found to be arranged in clusters and are equal in shape and size. The pots are found on the lower sides of the comb area not at the bottom.

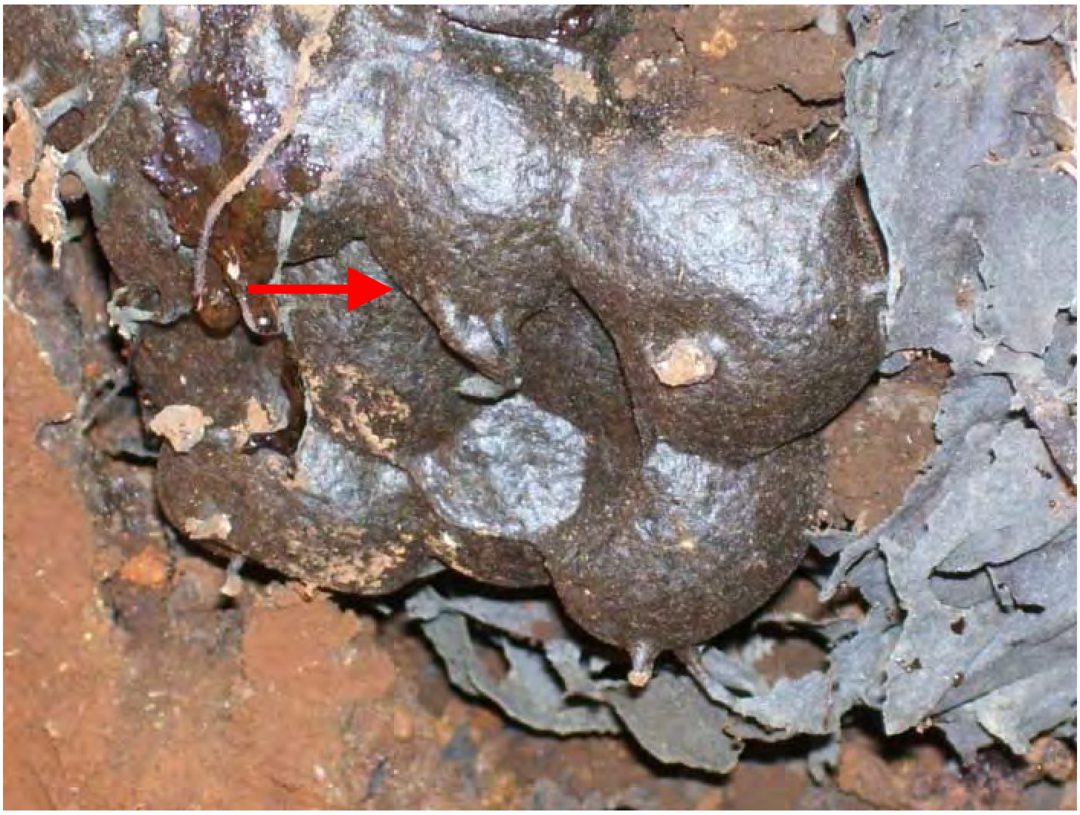


Figure 23. Honey and pollen pots

3.4.8 Drainage tube

The drainage tube is 16.5cm long and has a diameter of between 7- 12 mm in diameter. The drainage is very irregular in with. Some areas appeared narrower while others appeared broader. Tube also diverged into two in some areas.

Figure 24. Walls of drainage tube lined with layer of propolis

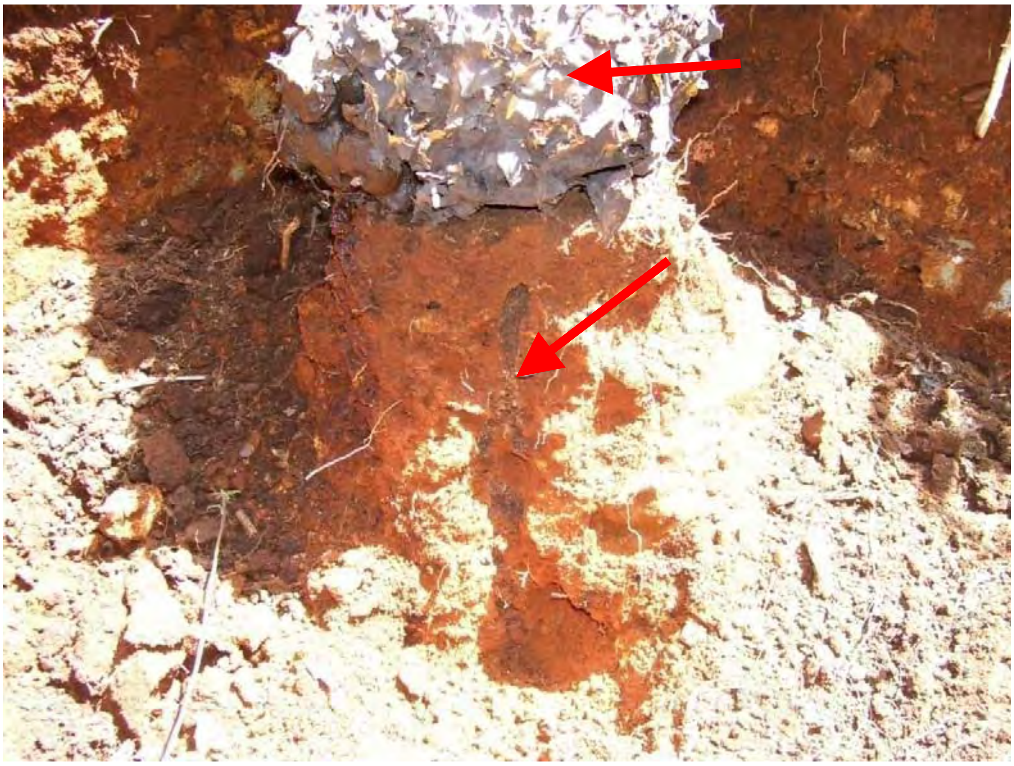


Figure 25. Drainage tube and nest cavity in soil

3.4.9 Behavior, ecology and distribution of *Meliplebeia becarri*

M. becarri do not manifest any aggressive reactions when nest is disturbed. The nest entrance is mostly guarded by 3-5 bees which are positioned slightly underneath the opening and retreats when ever a foraging bee is leaving or entering the nest. When the nests were excavated and opened, some of the bees left and flew around the nest and in its closed vicinity but did not exhibit any form of aggressive reactions. Bees begin a kind of absconding when forced to live in artificial nest. A few weeks after introduction into an artificial nest, all bees disappeared together with the queen. From close observation of the excavated nest, it is possible that *M. becarri* build their entrance tube and cavity. The gyne cells are almost 3-4 times the normal cells.

Table 3. Summary of measurements of *Meliplebeia becarri*

	Parameters measured	Number sampled	Range (cm)	Average (cm)	Shape	Colour
Nest entrance	Height of external entrance		0.5 - 0.6		Circular	Dark brown (propolis +soil particles)
	Thickness of wall and resin lining	3	1.5 - 2	1.7		
	Diameter of nest entrance		1 – 1.4			
	Length of internal entrance tube subteranean	5	27.5 – 34.5	30.3		
Nest cavity	Height	3	14 - 16	15		
	Diameter at brood area	3	12 - 13			
Batumen lining	Number	5	2 - 3			Brittle black
	Thickness		0.1			
Combs	Number of layers	4	6 - 8		Oval, round or heart	
	Diameter					
	Pillars	4	0.1-0.2			
Involucrum	Sheets of involucrum	5	8-12			Sticky light brown

	Thickness of involucrum	2	0.1	0.1		
Brood cells	Height		0.3 – 0.4		Spherical, oval	Dark yellow
	Diameter		0.2 – 0.3			
	Wall thickness		<0.1			
Storage pots	Height of honey pots		3-4			
	Diameter of honey pots		2.5 – 3.2			Shiny brown
	Height of pollen pots		3-4			
	Thickness of wall		<0.1			
	Diameter of pollen pot		2.5 – 3.2			
Drainage tube	length	1	16.5	16.5		
	diameter		7-1.2			

3.5 Nest architecture of *DACTYLURINA STAUDINGERI*

3.5.1 Abstract

Dactylurina staudingeri is the only stingless bee found with exposed nests. All the colonies seen were on fruit trees near living houses and in nearby bushes. The nests were fixed on tree at a height above 4m and attached to the tree branches. No nest was completely exposed to sun light rays. Combs are vertically constructed with doubled layer cells. The batumen layer is exceptionally constructed with many hard sheets. The workers bite when they are disturbed. The presence of some bird nests located much close to that of *Dactylurina* could probably be that the birds are taking advantage of the aggressive behaviour of *Dactylurina staudingeri.*

3.5.2 Nesting sites

Figure 26. A nest of *Dactylurina staudingeri* on the branch of a pear tree (*Persia americana).* Nest is shaded by a lot of leaves above. Notice the use of some lateral branches used as support through the nest cavity

Figure 27. Nest of *Dactylurina staudingeri* from an orange (*Citrulus*) tree.

3.5.3 Nest entrance

The nest entrance of *Dactylurina staudingeri* comprises 2 orifices: the large entrance with many other smaller entrances. The height of the main entrance is between 3-5cm high and the diameter between 3.5 – 5 cm wide. The small openings are very irregular in size and number, and can range from 16 – 27 in numbers (see Fig. 3 & 4).

The shape of the nest entrance is very irregular. The dimension of the orifice varies with the size of the nest. The nest entrance is always found at first lower quarter of the nest. The situation of the nest entrance is more or less constant in all nests we studied no matter the size. Bees coming into the nest do not go directly into the storage pots as in other species. They are obliged to pass through the layers or batumen and involucrum before reaching the brood cell area. The entrances are covered by pale yellow and sticky resins.

A network of pillars that builds up the multi-entrance and exit area, serves rapid attack as many bees can take off when disturbed. The pillars serve as platforms that allow many more bees to take off at once and make their attack rather than a single opening.

The guards and workers are always seen around the nest entrance, actively involved in construction works of the nest. The guards do not stay waiting for any enemies or intruder. The most import part of the nest consists of very hard and breakable layers. The inner involucrum is more rigid and soft. The thickness of this layer could be up to 6cm thick in some areas.

Figure 28. Complete nest of *D. staudingeri* showing position of nest entrance

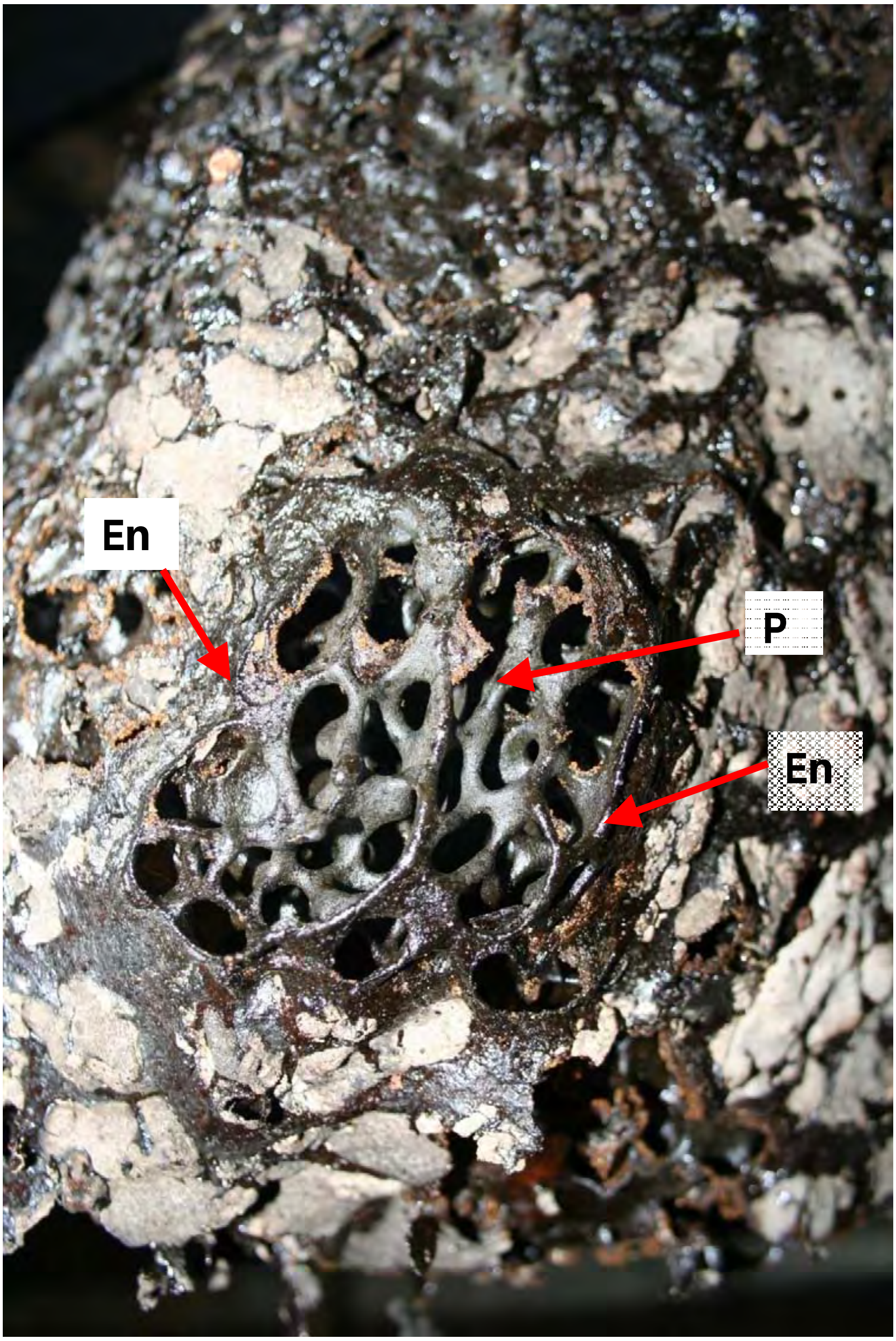


Figure 29.Details of nest entrance of *D. staudingeri*. EN- entrance wall, P-pillar

3.5.4 Batumen and invulucrum sheets

The brood area is always covered with layers of resins mixed with other plant materials such as leaves which play an important function in its development, thermal regulation and protection of nest against enemies and intruders. The batumen is a hard black thick structure made up of many linings (3-8) . The thickness of each batumen lining is < 0.1cm thick except for the main outer lining which is thicker. The outermost batumen lining covers the whole nest cavity leaving out just the openings at the nest entrance. They are usually 2-3 thin sticky involucrum layers. The involucrum lies between the batumen and the brood area. It covers the brood area completely.

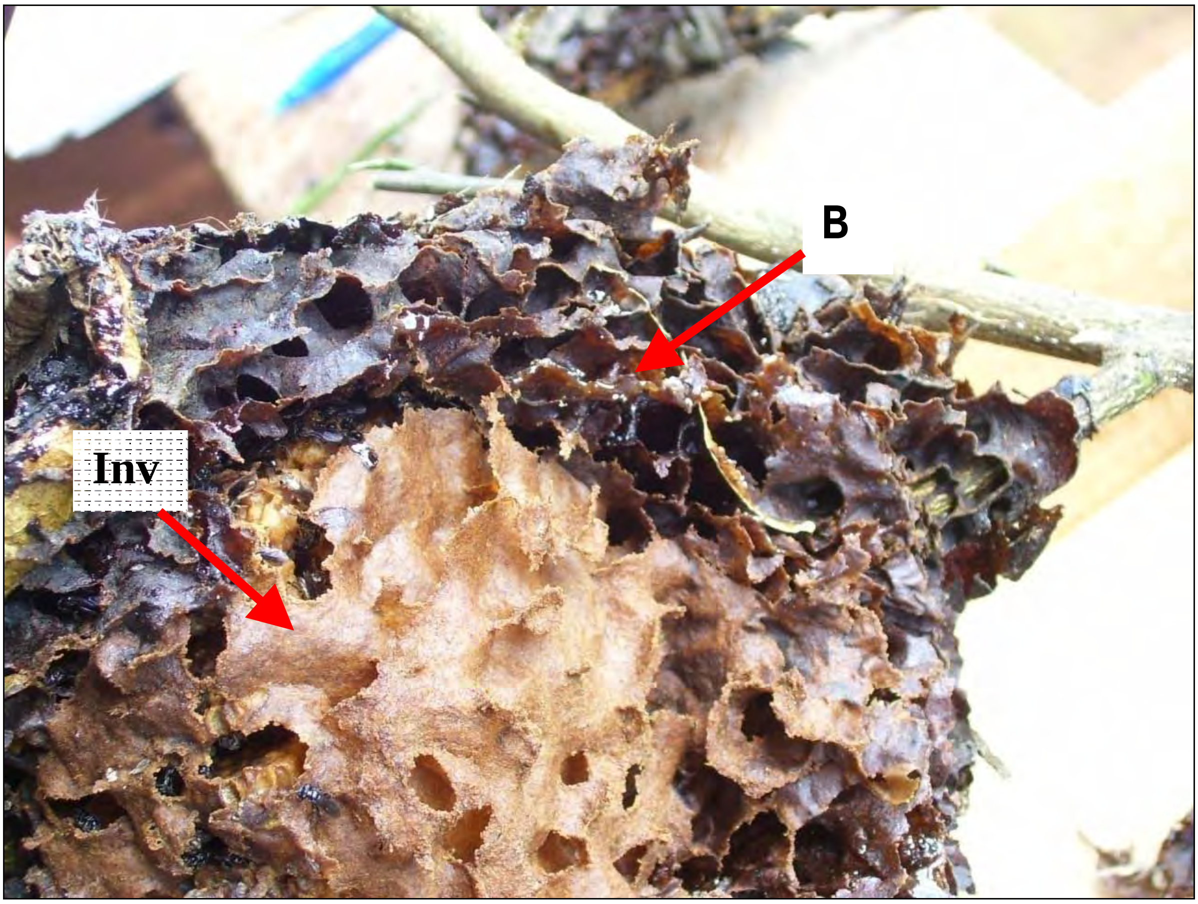


Figure 30. Partly exposed nest of *D. staudingeri* showing; Ba - Batumen, Inv- Involucrum

3.5.5 Storage pots

The storage pots are very irregular in shape ranging from spherical, oblong and conical. The honey pots and the pollen pots are very similar in size and shapes but differ in color. The honey pot is dark brown and the pollen pots are yellowish brow. The pots are 1.5-3cm high and 1.5-2cm in diameter.

Figure 31. Location and distribution of storage pots; **Hp**=Honey pot, Pp=Pollen pot

Pots are mostly located underneath directly below the lower portion of the brood area. A few pollen pots were also seen between the enormous batumen layers distributed unevenly all round the brood area (Figure 32).

3.5.6 Brood area

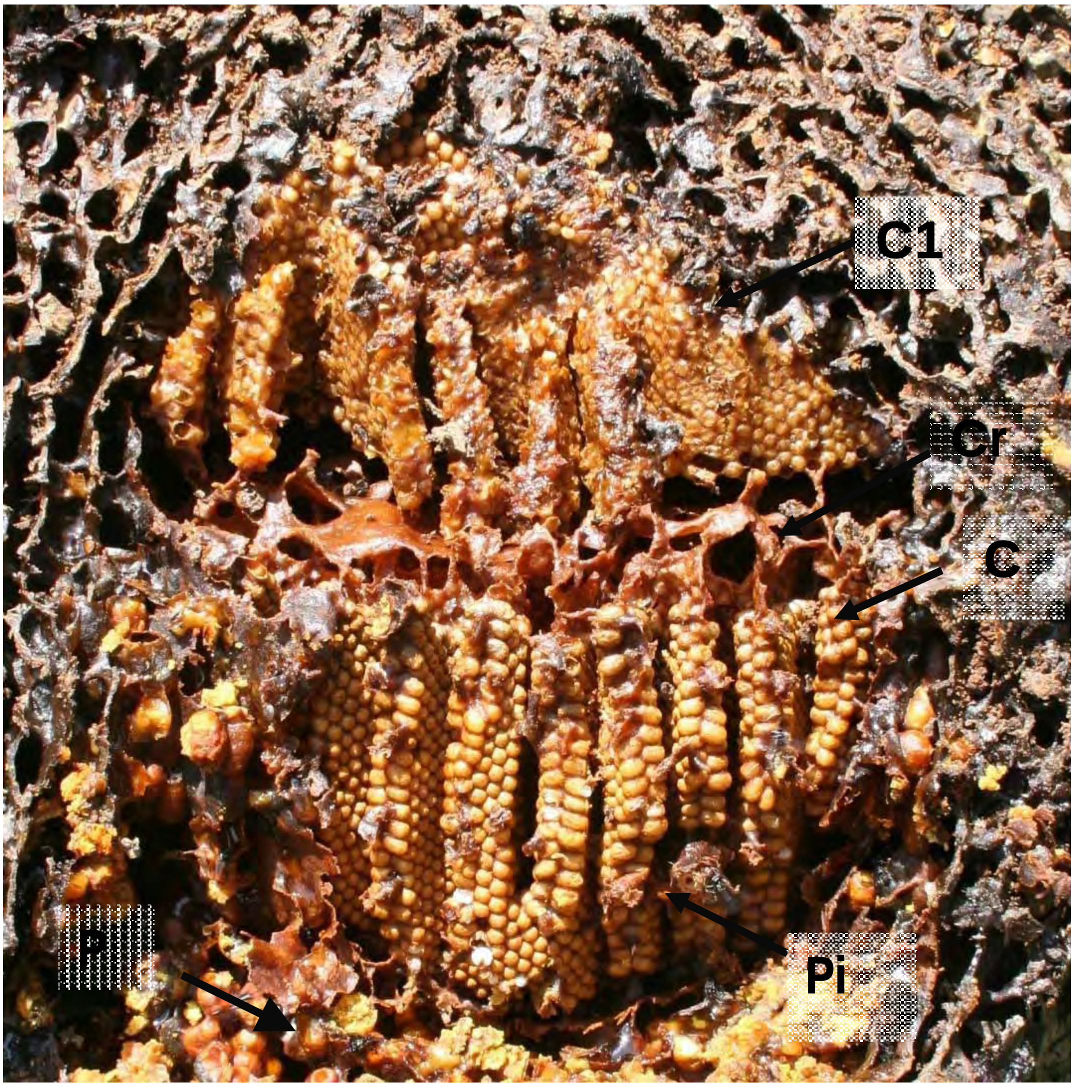


Figure 32. Brood area; **C1-**upper half of comb, **C2-**lower half of comb, **Cr** -Cerumen**, Pi-**Pillar, **P-**storage pots

The combs of *Dactylurina staudingeri* are vertically arranged with double layers (two single combs combined together). The brood area is divided into two portions: an upper portion and lower portion. The two portions are separated by a cerumen sheets constructed to differentiate the two. The cerumen seems to be a part of the involucrum between the portions. Each portion contains 6-10 doubled layers of combs and the numbers are not always the same. The gap between the two portions can be between 1-2cm in some areas.

Figure 33. Pillars separating combs are attached to on cells

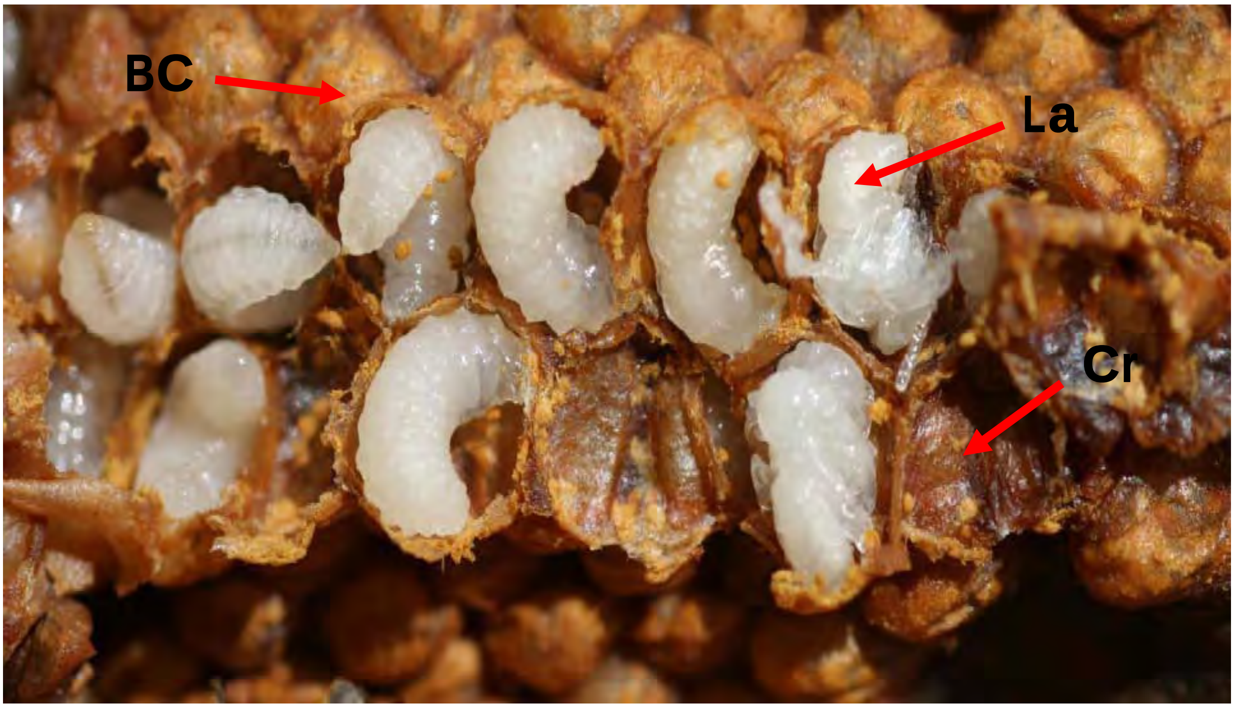


Figure 34. Brood of *Dactylurina staudingeri*; **BC**- Brood cell, **La**-Larvae, Cr= cerumen linking gap cells to one another.

3.5.7 Defense behaviour

As a defense strategy, *Dactylurine staudingeri* bites exposed skin parts and enters into the hairs, nostrils, eyes and ears. They would attack any other enemies similarly and scare them from coming closer to the nests. Their main weapon used for vigorous attacks comes from the design of the nest entrance. With multiple pillars at the openings of the nest entrances, many bees line up at the entrance prepared to come out in their numbers to attack any intruder when disturbed. It is difficult to work with this species without protecting exposed body parts.

Table 4. Summary of measurements taken for *D. staudingeri*

	Parameters measured	Nest 1	Nest 2	Nest 3	Nest 4	Average	Shape	Color
Nest cavity	Height of nest (cm)	22	34	31	24	27.75		
	Diameter of nest(cm)	16	22	19	14	17.75		
Batumen lining	Number of batumen	3-4	3-8					Blac k
	Thickness of batumen (cm)	0.1						
Combs	Number of combs	6/6	9/10					
	Diameter of combs (cm)							
Involucrum	Number of involcrum	2	3				Light brown	
	Thickness of involucrum (cm)		<0.1					
Brood cells	Height of cell (cm)		0.3-0.5(5)					
	Diameter (cm)		0.2-0.3(5)					
Storage pots	Height of Honey pots (cm)		1.5 - 3				spherical, oblong and conical	Dark brown
	Diameter of honey pot (cm)		1.5 - 2					
	Height of pollen pot (cm)		1.5 - 3					Yellowish
	Diameter of pollen pot (cm)		1.5 - 2					

3.6 Nest architecture of *MELIPONULA (AXESTOTRIGONA) FERRUGINEA*

3.6.1 Abstract

Meliponula (*Axestotrigona) ferruginea* belong to the genus, Meliponula and subgenus Axestotrigoa: The species was first described by LEPELETIER (1836) and MICHENER (2000) recently. In Cameroon the species has been collected in the northern parts of the country but without any attempts to describe the nest architecture. Our stingless bee survey from the Bamenda highlands afromontane forests of Cameroon reveals that this species can either nest in tree trunks or in abandoned traditional hives. Interestingly, two of the four colonies found during the survey period nested in traditional hollow hives originally baited to attract honeybees. The nest entrance ranged from 1 - 1.5cm in diameter and the external entrance tube could be extended to 2cm in high outward. The external entrance tube can go up to 5cm in length depending on the thickness of the tree trunk. The size of brood area depends on the age and condition of the nest: Length could be up to 75cm and up to 14cm for the diameter with 10 - 14 combs.

3.6.2 Nesting sites

Figure 35. Tree trunk with the nest of *Meliponula ferruginea*

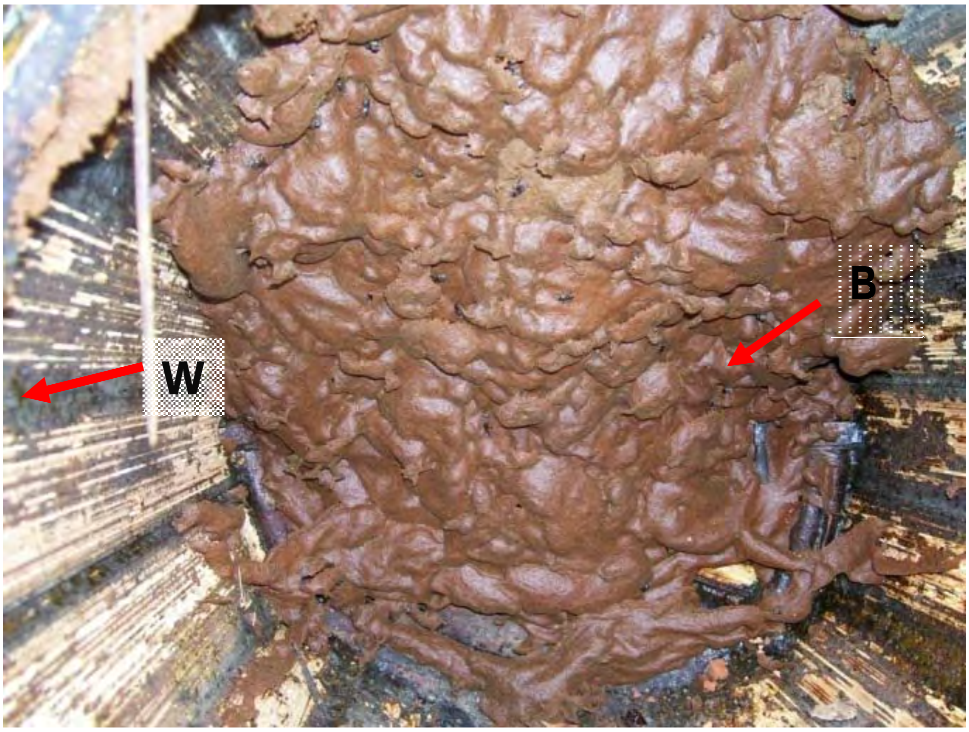


Figure 36. Nest of *Meliponula ferruginea* in traditional hive: W= wall of traditional hive constructed with bamboos, **Ba =** Batumen layer surrounding the brood area

These bees prefer to use tree trunks between 1.5 - 2m above the ground for their nests. The two tree trunk nests observed were all located on trees with circumference of 35cm and 37cm. The trees were also located in open areas of the savanna forests with fewer tree canopies which could possibly obstruct sunlight rays from touching the nest entrance. Colonies in traditional hives confine their nest to a particular portion of the hollow cavity and protect the colony with a batumen lining separating the nest from the rest of the cavity. They used just about a third of the cavity of the traditional hive. From the colony that was placed in observation hive, it is clear that these bees do not solely depend on already existing cavities in the trees to place their nests. They are capable of creating a cavity of their own.

3.6.3 Nest entrance

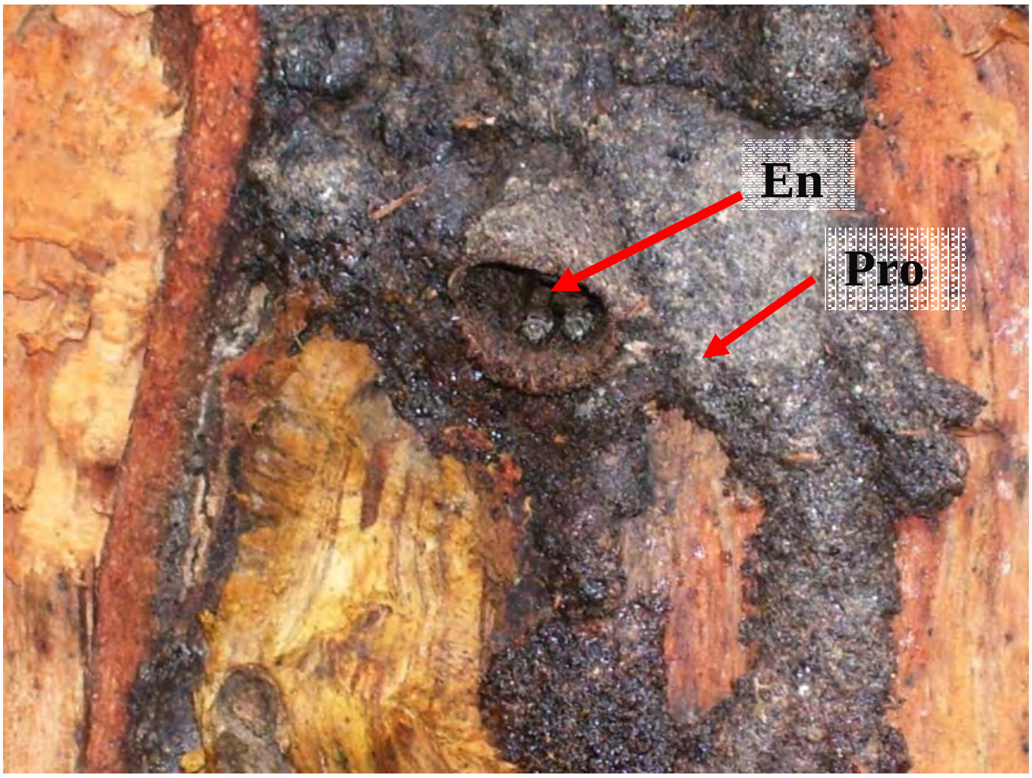


Figure 37. Nest entrance of *Meliponula ferruginea* on tree trunk.

Notice the outer tube of 2cm length. The diameter of the entrance is 1- 1.5cm and the length of the external tube is 5cm long. The surrounding of the nest entrance is smeared with propolis.

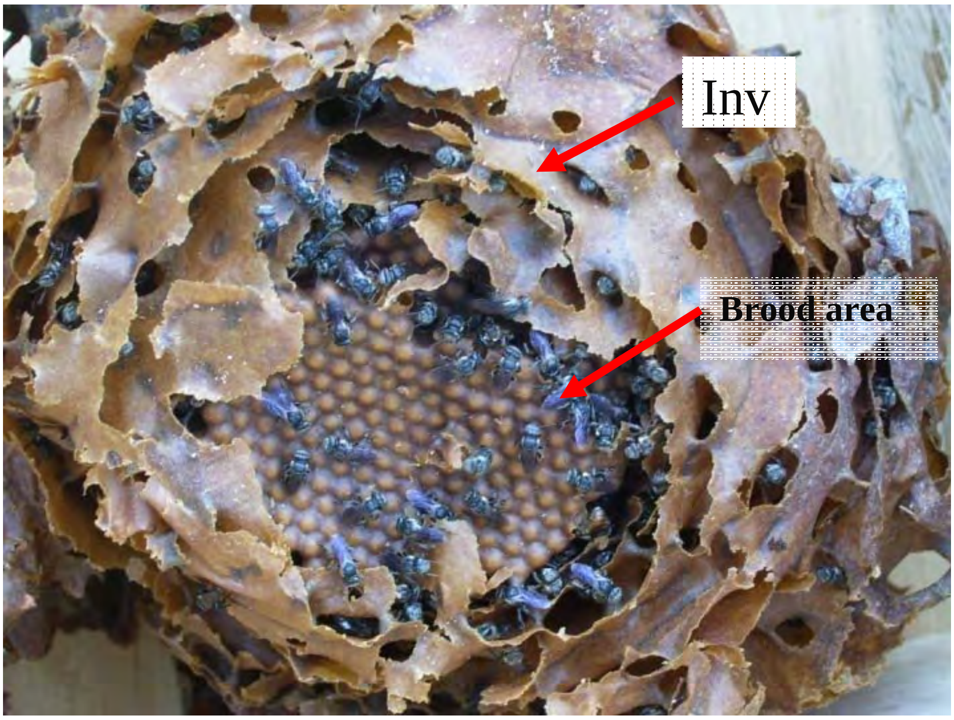
Figure 38. Nest entrance of *Meliponula ferruginea* in traditional hollow hive.

No outer tube projection and very little propolis outside the entrance compared that found on the entrance on tree trunk. Entrance does not lead directly into the brood area but to the batumen. For nests in tree trunk, no batumen layer was found.

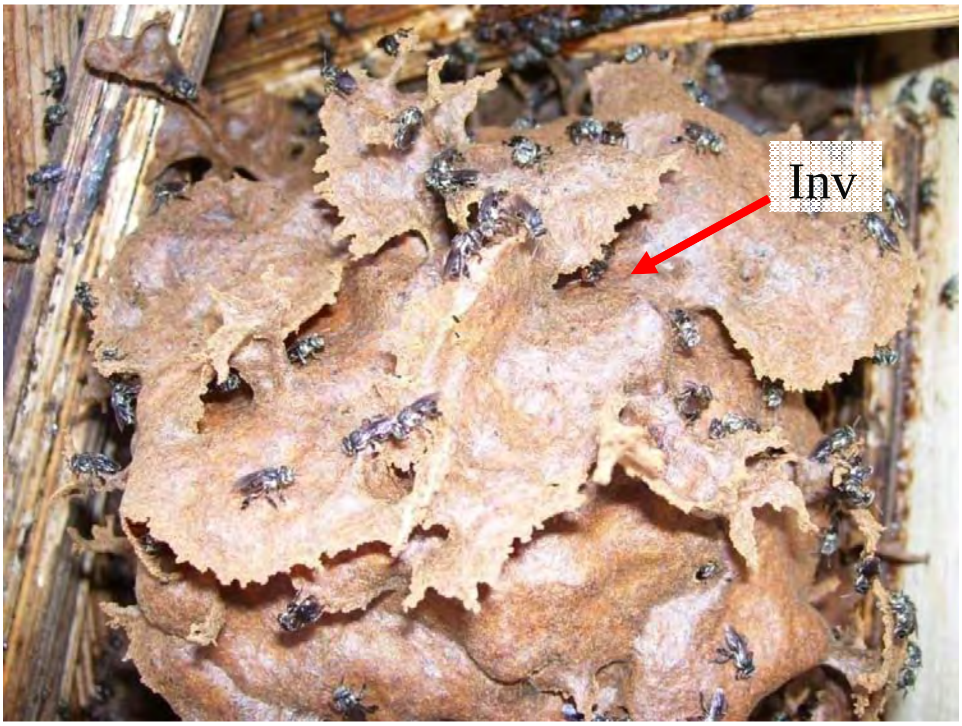
3.6.4. Nest cavity

Figure 39. Nest cavity of *Meliponula ferruginea* in tree trunk. Portion of trunk removed to expose the nest in the cavity.

3.6.5. Involucrum



Figures 40. Sheets of involucrum surrounding the brood area. Inv = Involucrum sheet



Figures 41. Involucrum sheets surrounding the brood area. Inv = Involucrum sheets

The involucrum consists of 5-7 sheets. Each sheet is less that 0.1cm thick. Sheets are attached to each other and to the brood comb by a 2-3mm long pillar. The sheets are sticky apparently composed of wax and other substances.

3.6.6. Brood area

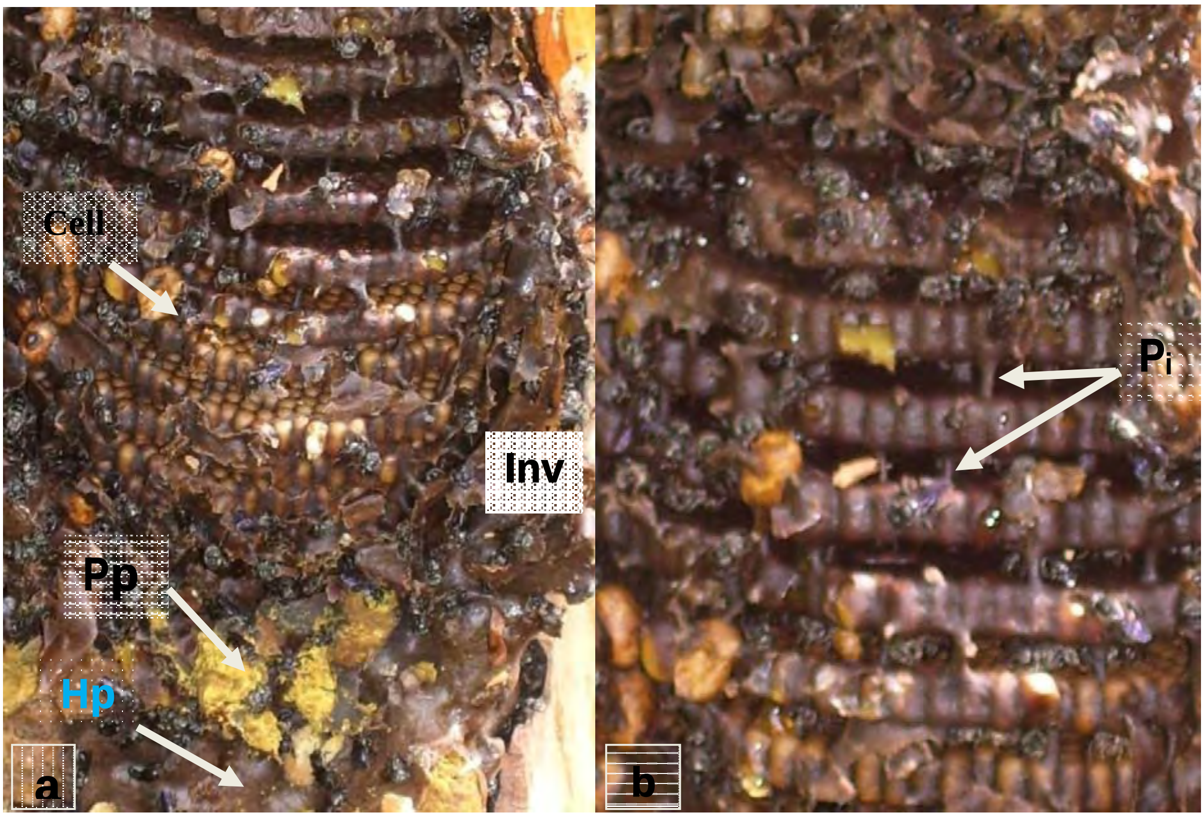


Figure 42 a & b. Combs of *Meliponula ferruginea* arranged in horizontal layers

P_i = Pillar, P_p= Pollen pot, H_p=Honey pot, Inv = Involucrum

The storage pots are mainly found underneath and above the brood area. The pots are clustered together with similar shape and size.

Figure 43. Combs of *Meliponula ferruginea*

The combs are oval, round or heart shaped with diameter between 7-9cm. The number of combs per colony could be between 8 and 18. Comb number depends on the size, environment and age of the colony. Colonies in tree cavities seems to have higher number of combs than the colonies in hives. Cell measured 1cm high and 0.6 cm in diameter. Cells are spherical in shape.

3.6.7. Defensive behaviour

Meliponula ferruginea are generally very calm bees. However, they are capable of fighting against intruders into their nests by biting and chopping off the wings. This was observed with honeybees that were attracted into the nest by spilt honey inside the nests of *M. ferruginea*. Sometimes the nest entrance was sealed off with propolis to prevent any intruder from entering the nest. Generally, these bees are very easy to handle though complex to investigate tasks related to brood production during observations in artificial hives.

Table 5. Summary of measurements take for *Meliponula (Axestotrigona) ferruginea*

	Parameters measured	Nest 1	Nest 2	Nest 3	Nest 4	Shape	Colour
	Nest height above groundn (cm)	1.5m	2m	3m	2m		
Nest Entrance	Height of external entrance (cm)	1.5	2				
	Diameter of nest entrance(cm)	1	1.5	1.2	1.2		
	Length of entrance tube(cm)	5					
Nest Cavity	Length of nest	75		35			
	Diameter of nest(cm)	14		14			
Batumen lining	Number			1			Sticky Brown
	Thickness (cm)			1.5			
Involucrum	Number	5		7			Sticky Brown
	Thickness (cm)	0.1					
Pillar	Length (cm)	0.2		0.2			
Combs	Number of combs	18		8		Heart, oval or circular	
	Diameter of combs(cm)	8 and 9		7			
Cells	Height of cell(cm)	0.3		0.3		Oval	
	Diameter(cm)	0.2		0.2			
Storage pots	Height (cm)	1.2		1.3			
	Diameter (cm)	1		1			

3.7 Nest architecture of *MELIPONULA BOCANDEI*

3.7.1 Abstract

Meliponula bocandei nests in both tree trunks and in empty traditional hive. They prefer tree trunks at breast height greater than 50cm. This species seems to enjoy warm temperature areas. All four colonies seen (two in hives and 2 in tree trunk) were in savanna bushes with sparse tree distribution. The nest entrances of this species are quite varied in shape, size and number. No external nest entrance tube was seen in either of the cases. The diameter of the main entrance ranged from 2-3cm.The batumen lining is hard and thick (1-2cm thick) and made of propolis, soils and leaves. Involucrum is present is patches and confined to particular areas with up to 3 sheets in some areas. Cells are spherical with distinctive colours for the older cells and the new cells. Cells are grouped into many different clusters.

The pollen pots are found at the surface of the brood while the honey pots are found underneath. Pots are of different shapes.

3.7.2 Nest Entrance

Figure 44. Nest entrance on large tree trunk

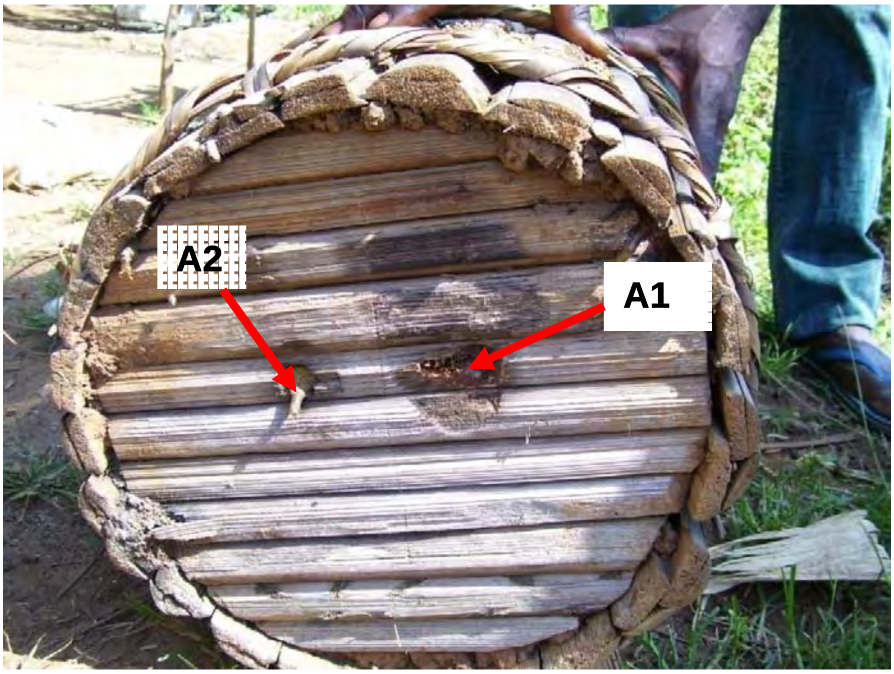


Figure 45. Nest entrance of *meliponula bocandei* and Liotrigona bottegoi on hollow hive: A1 = nest entrance of *Meliponula bocandei;* B2 = nest entrance of *Liotrigona bottegoi.*

Figure 46. Nest entrance of *Meliponula bocandei* on a traditional hollow hive

3.7.3 Batumen lining

Figure 47. Batumen covering the back part of the nest. Ba = Batumen, Bam-Bamboos used for the hive construction.

The whole nest of *Meliponula bocandei* occupied just about a third of the total area of empty traditional hive. The entire colony inside the hive is protected all round by the batumen lining.

Figure 48. Batuemn lining covering the nest removed to reveal the brood area.

The batumen is very hard and made up propolis, leaves and soil. It could be as thick as 2cm in some areas and as thin as 1cm in other places. The batumen is perforated with small holes which are very unevenly distributed and irregular in sizes.

3.7.4 Involucrum

Figure 49. Patches of Involucrum sheets found at some spots of the brood area.

The number of sheets could be up to 3 at some areas. The sheets are thin and sticky (<01cm thick) and almost transparent.

3.7.5 Brood area

Figure 50. Old and new brood cells of *M. bocandei*. A = Older cells, B=Newly oviposited cells, C= cell under construction.

Older cells are creamy yellowish in colour as the wax layer of the cocoon was removed by the workers while the new cells, both under construction and newly oviposited are brownish in colour. The cells are spherical in shape.

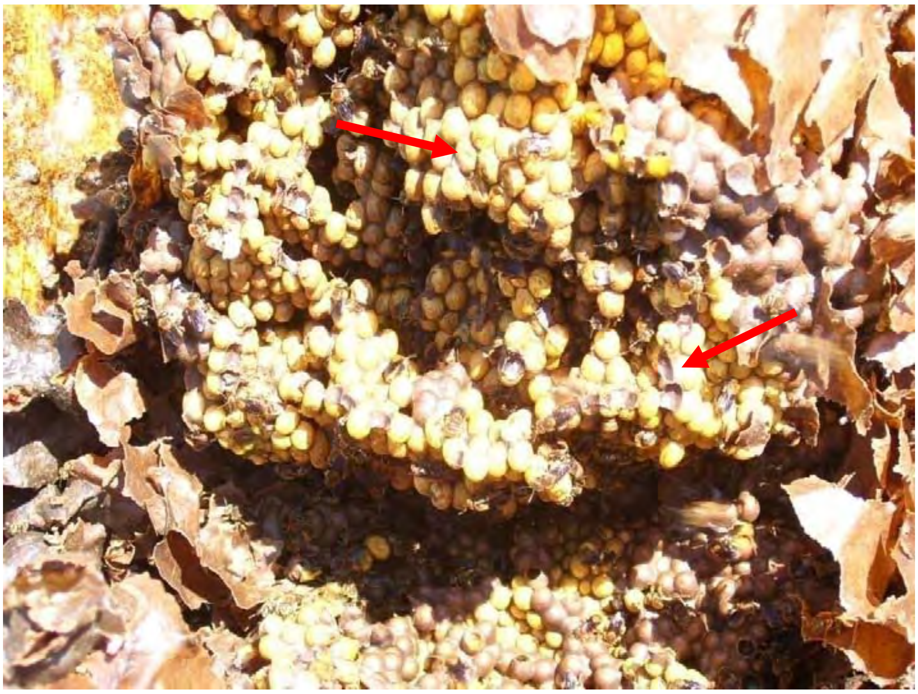


Figure 51. Different blocks of clustered cells grouped together in disorganised arranagements. Cells seems to be packed in a discontinuous manner with gaps in between groups.

3.7.6 Storage pots

Figure 52. Pollen and honey pots of *Meliponula bocandei*

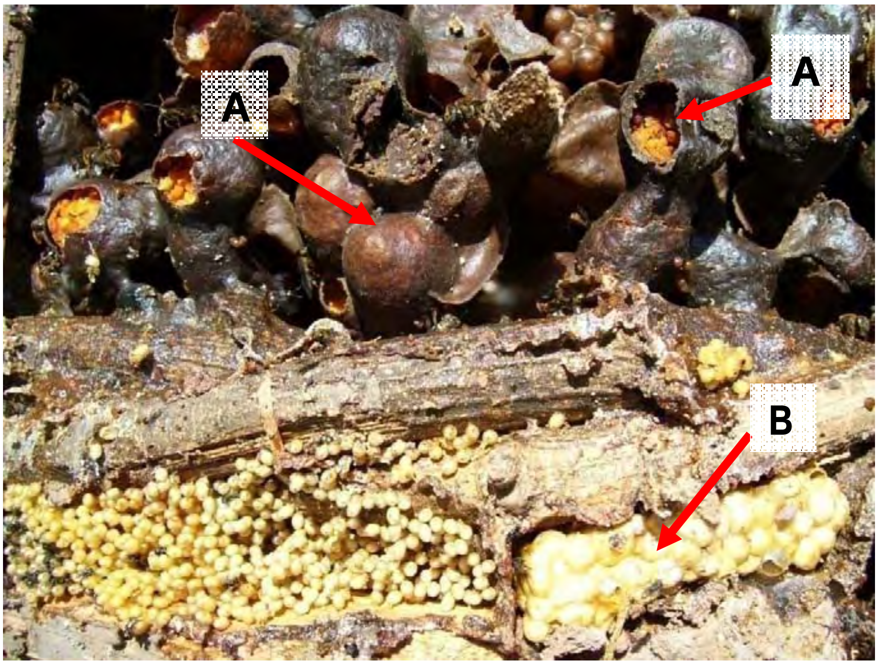


Figure 53. *Meliponula bocandei* living with *Liotrigona bottegoi* in same hive
A= storge pots of *M. bocandei*, B=Storage pots of *Liotrigona bottegoi*

Liotrigona nested in the crevicess of the bamboos using in construction the traditional hive while Meliponula bocandei occupied part of the inner hollow hive.

3.7.7 Defensive behaviour

These bees are very docile and are not aggressive. During excavation no case of attack was observed either on the exposed parts of the body. The bees were just found flying out of the hive or around without landing.

Table 6. Summary of measurements taken for *Meliponula bocandei*

	Parameters measured	Number Sampled	Nests	Shape	Colour
Nest entrance	Height of external entrance (cm)			Varies	
	Diameter of nest entrance (cm)	3	2 - 3.5		
	Length of entrance tube (cm)				
Nest cavity	Height of nest (cm)	1	20		
	Diameter of nest(cm)	1	18		
Batueme lining	Number of batumen	1	1		Brown
	Thickness of batumen(cm)	1	1-2		
Involucrum	Number of involcrum		1-3		Transpare nt brown
	Thickness of involucrum(cm)		<1		
Brood cells	Height of cell(cm)			Spherical	Cream yellow or brown
	Diameter (cm)				
Storage pots	Honey pot- height(cm)		3-4	Varied forms	
	Honey pot - diameter(cm)		2--3		
	Pollen pot- height(cm)		3-4		
	Pollen pot - diameter(cm)		2-3		

3.8 Nest architecture of *LIOTRIGONA BOTTEGOI*

3.8.1 Abstract

This was the most abundant of the six species of stingless bees found in the Bamenda highlands afromontane forests. This species is capable of nesting in a wide variety of sites: ranging from walls of mud houses, abandoned traditional hives, bamboos and roofs of old houses. However, a majority of the registered colonies (more than 75%) were found on mud walls of houses. The population of a colony is between 100 and 300 individuals. The nest entrance is conical in shape and the entrance diameter ranged between 5-8mm with very thin walls. The nest entrance tube always projects 2-3cm outwards.

Like most cluster nesters no batumen layer was found in any of the colonies but a sheet of involucrum was seen covering the storage pots in one case. Brood cells are yellowish with 2-3mm in diameter and linked to each other by a short pillar which is less than 1mm long. Pots were much larger than the brood cells (1cm in diameter) and were not differentiated into separate pollen and honey pots. No link existed between the brood cells and the storage pots. Honey and pollen pots are generally in separate elongated clusters, though one or two honey pots can be found in the cluster of pollen pots. Pots and cells are supported by tiny pillars (1-3mm) fixed to the surface of the wall or to the crevices. The shape of the pots were irregular and brownish yellowish in colour for pollen and almost transparent for honey pots.

Liotrigona bottegoi do not react to any form of manipulation. When disturbed they merely retreated into the nest without any display of defense. They are generally not aggressive but further defense mechanisms shall need to be investigated.

3.8.2 Nest entrance and nesting sites

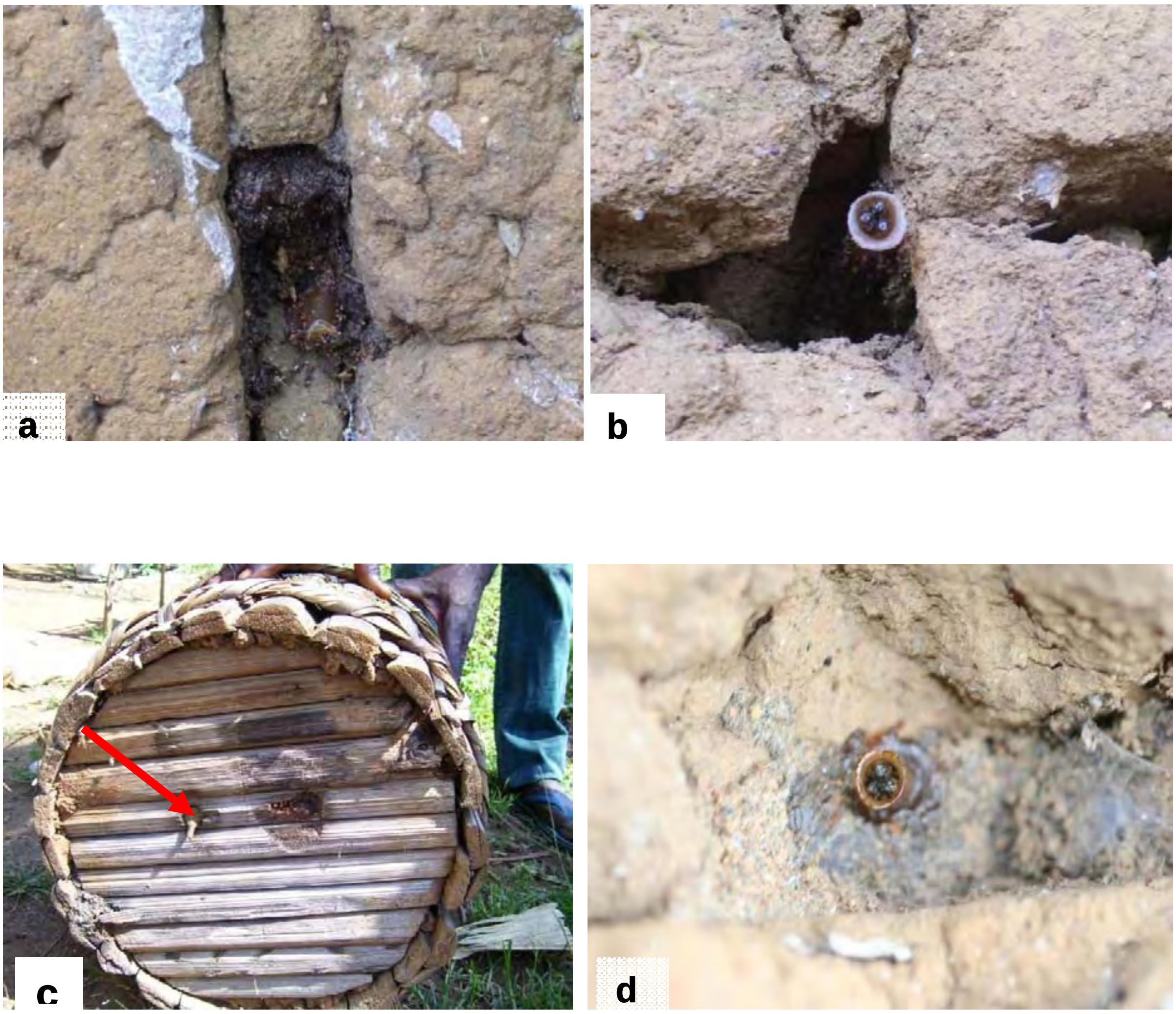


Figure 54 a, b, c & d: Different shapes of nest entrances of *Liotrigona bottegoi*

Nest entrances vary in sizes, lengths and diameters but are generally conical shape. Though narrow, 3-4 guard bees can be found guarding the entrance at any time.

3.8.3 Brood cells

Figure 55 a, b & c. Cluster cell arrangements of *Liotrigona bottegoi:* a= cells are almost isolated, b= cells packed together (older cells), c= younger cells packed together

Brood cells are constructed on a single plane or up to 3 or 4 layers clusters. Younger cells are yellowish in colour while older cells are pale yellow. They are attached to each other and to their plane by short pillars. Cells are compact together such that the workers bees can only walk on the surface and not between.

3.8.4 Storage pots

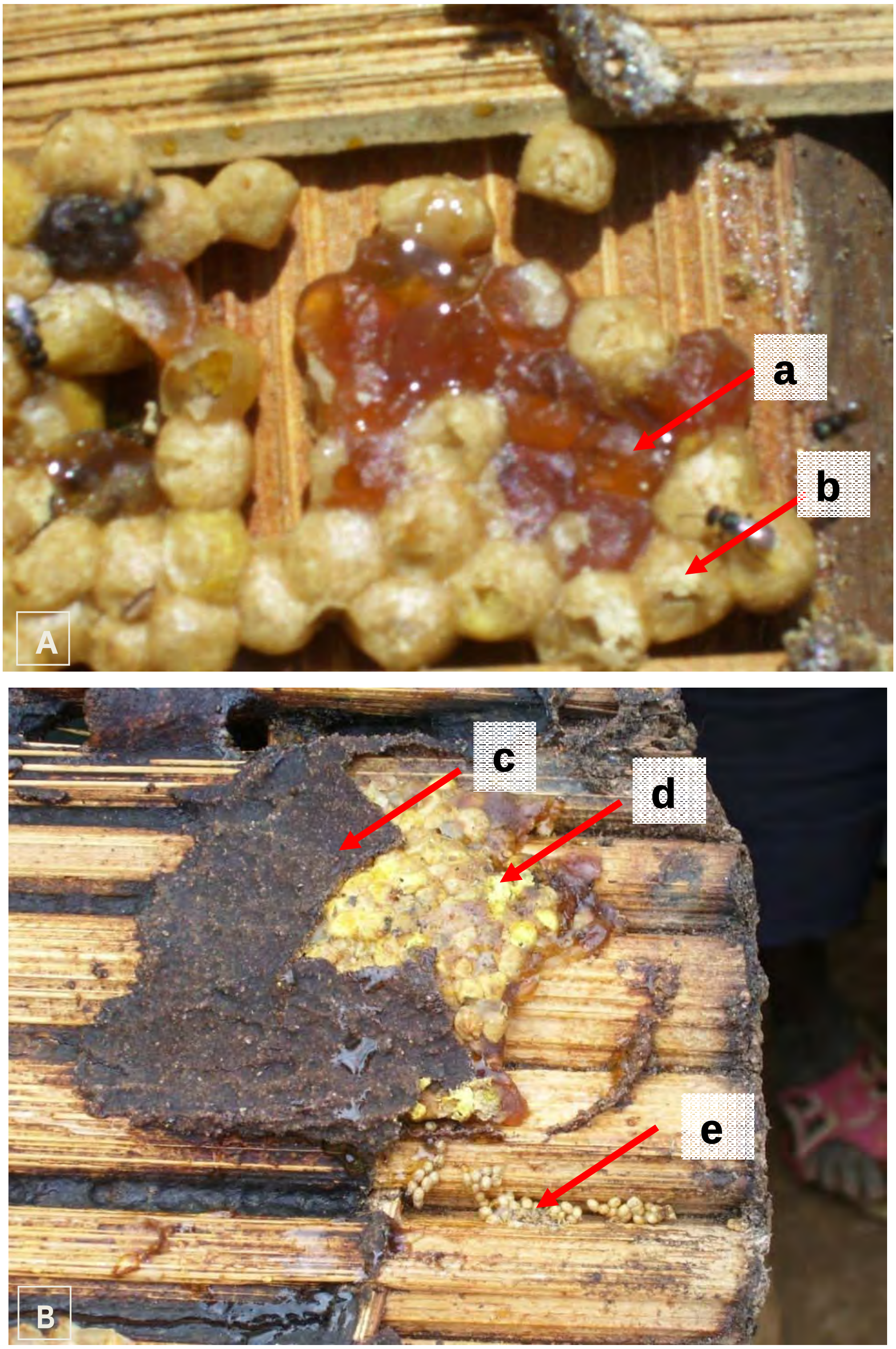


Figure 56 A & B: Pollen and honey pots arrangement of *Liotrigona bottegoi*
A=honey pot, b= pollen pot, c= Batumen or just protective layer, d=storage pot, e=cells

3.8.5 Defense behaviour

Bees are not aggressive. During manipulation they were just flying around without any attack.

Table 7. Summary of measurements for *Liotrigona bottegoi*

	Parameters (cm)	Number sampled	Range	Shape	Colour
Nest entrance	Height of external entrance		2 - 3	Conical	
	Thickness of wall		0.1		
	Diameter of nest entrance	8	0.5-0.8		
Involucrum	Sheets of involucrum	1 on storage pot		Black	
	Thickness of involucrum		0.5		
Brood Cells	Height		0.3-0.4	Round	Yellow
	Diameter		0.2-0.3		
Storage pots	Height of honey pots		1-1.2		Transparent brown
	Diameter of honey pots		1		
	Height of pollen pots		1-1.2		Yellow
	Diameter of pollen pots		1		

3.9. Nest architecture of *HYPOTRIGONA GRIBODOI*

3.9.1. Abstract

Two nests of *Hypotrigona gribodoi* were excavated during the study period. The colonies nested in tree branches with diameters of 20 and 28cm. Cells are constructed separately without any regular plane. These are cluster makers with no combs. Cells are spherical at the top and bottom revealing an uneven appearance of the surfaces. The main nest entrance is narrow with a diameter of 1-1.2cm that can allow the passage of 3-5guard bees at a given time. Smaller escape entrances can develop around the main entrance when colony is under stressed. Dirt from the nest is simply thrown down from the nest entrance very early in the mornings every day, resulting in small heap below the entrance.

3.9.2. Nest entrance

The outer nest entrance of *H gribodoi* before the branches were cut was just a single hole. Days after the numerous tiny secondary entrances developed around the original outer entrance (fig 56 & 57). The almost circular shape of the original outer entrance starts widening up (fig 58). The new outer entrance (fig 58) is broader with a funnel like structure which is irregular brim .

The secondary entrances are in layers and cover a considerable area around the main entrance. They are interwoven and with each measuring less between 2-3mm in diameter.

Figure 57. Main nest entrance of *Hypotrigona gribodoi*

Figure 58. Smaller secondary entrances of *Hypotrigona gribodoi*

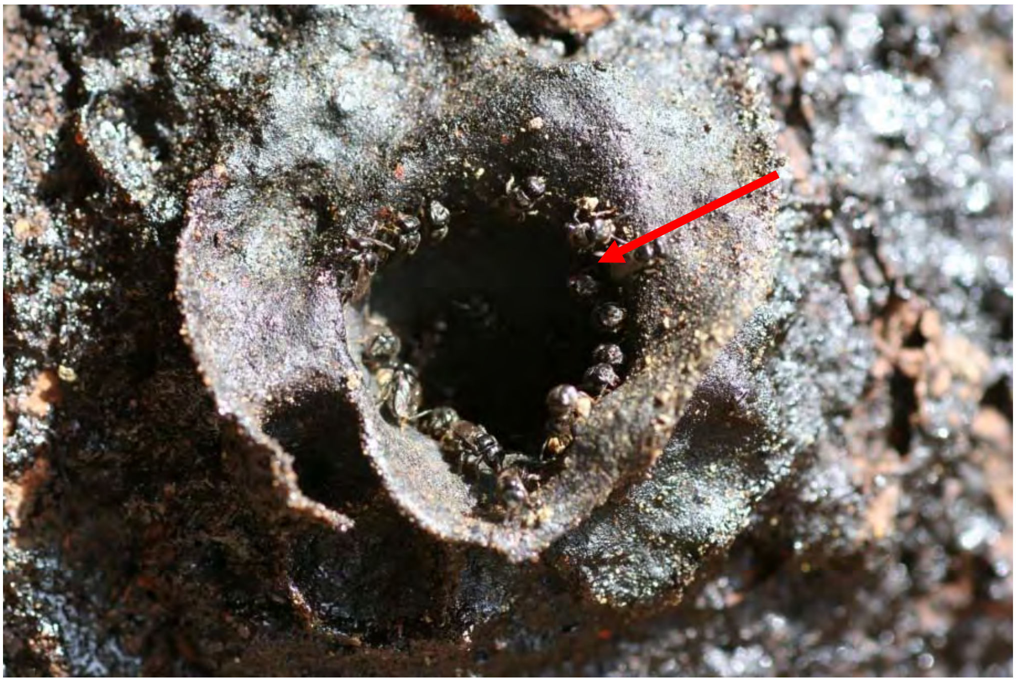


Figure 59. Nest entrance after tree branch has been tempered with.

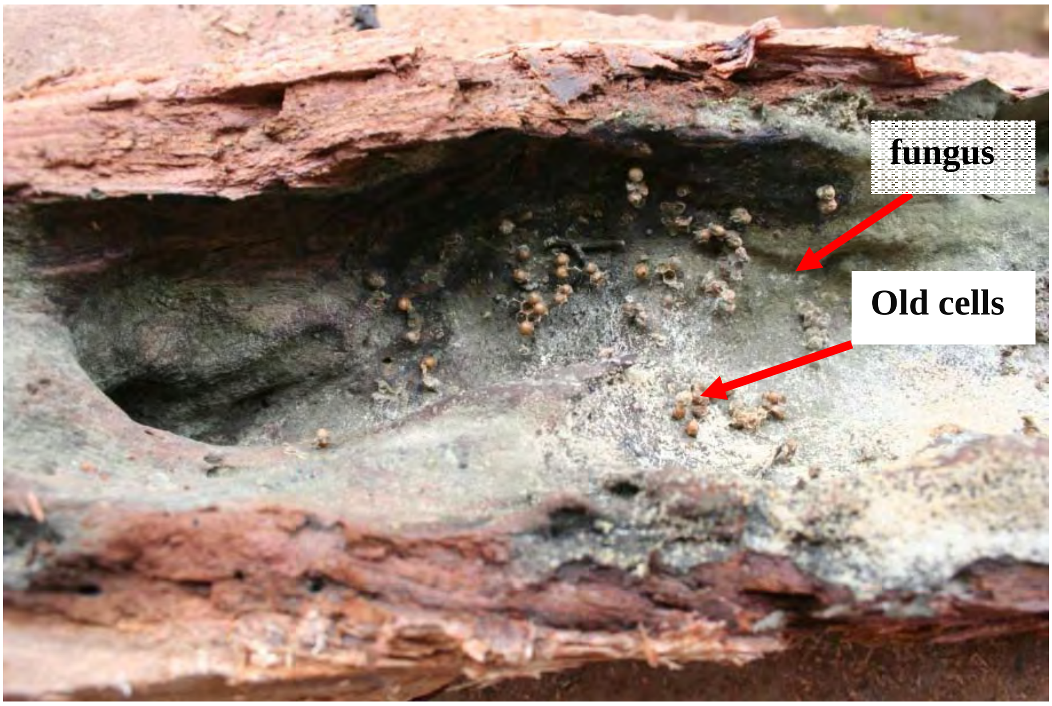


Figure 60. Inner tree cavity with fungus and some old brood cells after excavation

Hypotrigona gribodoi lives with fungi on the walls of the tree cavity. The fungus has no direct contact with the brood area. This was seen from the two excavated nests. The brood cells attached to the walls by spikes which dimensions depend on how far the brood is from the tree wall. Numerous individual cells were seen projecting directly from the walls with short pillars sustaining them. The bulk of the brood concentrated at a particular location but small groups of cells could be found at some locations inside the cavity sometimes attached to the wall just by tiny spikes or pillars.

3.9.3. Involucrum

Figure 61. Wax layer enveloping brood area of *Hypotrigona gribodoi* after excavation

Normally, broods areas are not protected by any envelop. This envelop was found after the colony had been under serious stress. The envelop is very sticky and made up of cerumen.

3.9.4 Brood area

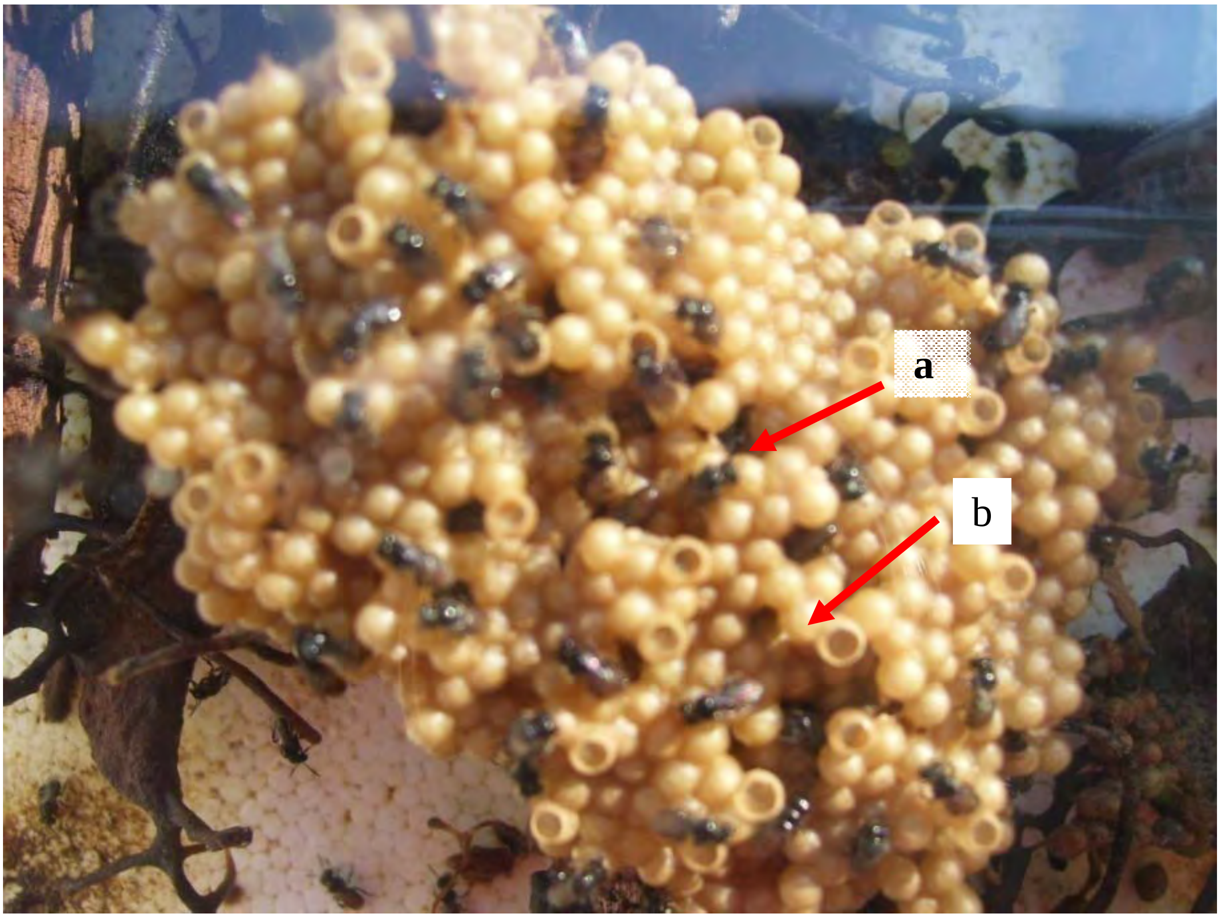


Figure 62. Cluster arrangement of both sealed and open cells *Hypotrigona gribodoi*.
a= sealed cell, b= cell under construction (open cell)

Cells are clustered together by cerumen with no pattern of organization. Older cells that have been oviposited and sealed are found beneath while new cells under construction are found on the surface. Cells can be oval or oblong in shape. Meanwhile the storage pots are circular or shapeless.

3.9.5 Storage pots

Storage pots are situated on the sites below the brood cells. The pots are all similar in size and shape. The honey pots are light brown while the pollen pots are dark brown in colour.

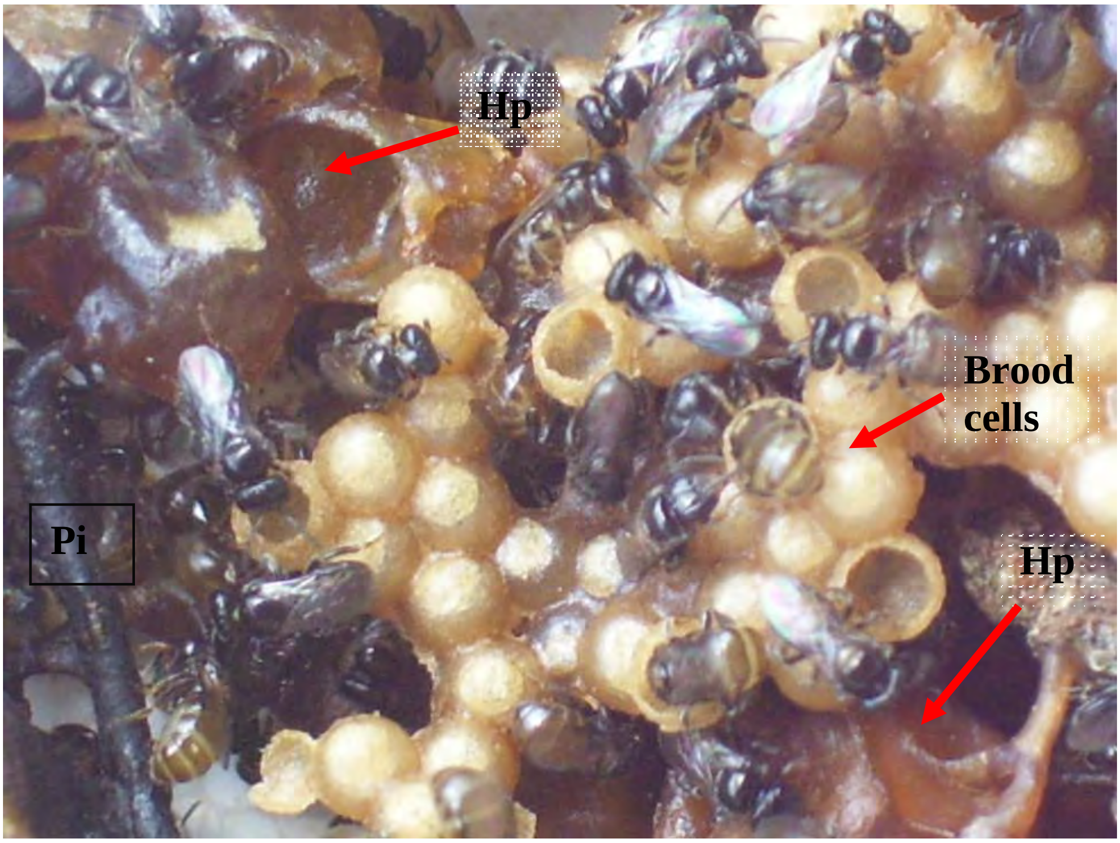


Figure 63. Storage pots of *Hypotrigona gribodoi*. Hp= enlarged honey pots, Pi= pillar

Storage ports are mostly at the edges of the brood cells. Honey pots are brownish and almost transparent while the pollen pots are brownish yellowish. Storage pots are anchor to walls of hive by long pillars.

3.9.6 Defense behaviour

These bees were never seen attacking parts of the body but were seen fighting and biting on the wings of another bee trying to collect spilt honey from their nest.

Table 8. Summary of measurements of *Hypotrigona gribodoi*

Parameters measured(cm)	**Nest 1**	**Nest 2**
Height of external entrance	1.2	0.5
Diameter of nest entrance	1.1	1
Length of entrance tube	5	6
Thickness of wall surrounding brood	0.1	Not found
Height of cell	0.3 - 0.4	0.3-0.4
Diameter of cell	0.2	0.3
Height of pollen pot	1.2	1.3
Diameter of pollen pot	1	1
Height of honey pot	1.2	1.3)
Diameter of honey pot	1	1

3.9.7 Discussion

This study has possibly brought out all or a majority of the existing species of stingless bees in Bamenda Highlands. The three species of the genus Meliponula (*Meliplebeia becarri, Meliponula ferruginea and Meliponula bocandei*) in Bamenda afromontane forests exhibits inter-specific differences in size, colour and nest entrance characteristics similar to those found in Uganda (KAJOBE, 2006). Among the six species of stingless bees found in the Bamenda afromontane forests, *Meliponula bocandei* was the largest in size while *Liotrigona bottegoi* was the smallest. Contrary to KAJOBE (2006), the nests of *Meliponula bocadei* were never found in the ground. Nests were found in traditionally hives and in large tree trunks.

As observed by MICHENER (1974) and ROUBIK (1989), nesting site preferences such as trees, ground and wall crevices were similar to most species in Bamenda highlands. Though in addition to these nesting sites, a few colonies were found nesting in abandoned traditional hives baited for honey bees. Nest site specificities only occurred with *Liotrigona bottegoi* where all nests were found on mud walls in Bamenda afromontane forests area.

Colonies of *Liotrigona bottegoi* exhibited monospecific nesting aggregation with their nests located much closed to each other on mud walls. This kind of nest aggregation has been reported by ELTZ et al. (2003). Unlike NAMU (2008) and KAJOBE (2006), *Hypotrigona gribodoi* nests were never found in termite mounts. Nests were only found in trees trunks in the Bamenda highlands.

Meliplebeia becarri was the only species that was found nesting in ground. This is one of the very few subterranean nests of stingless bees to be studied in Africa recently. ARAUJO (1963) studied the subterranean nests of 2 African species, *Meliplebeia tanganyika medionigra* and *Plebeilla landliana*. The large voluminous involucrum in *M. tanganyika* was also present in *M. becarri*. Similar to the study done by FLETCHER & GREWE (1981) on *Trigona denotti* subterranean nests, all studied nests of *Meliplebeia becarri* were solitary and non of the excavated nests was found in termite mounts.

Our study on the nests of *Dactylurina staudingeri* shows similarities in cell sizes with that of DARCHEN & PAIN (1966). However, contrary to DARCHEN & PAIN (1966), storage pots in *D. staudingeri* were predominantly located underneath the vertical combs and not particularly in shells of the batumen as mention the their study. The multi pillar nest entrance of *D. staudingeri* and the functions was never studied. *D. staudingeri* also seems to exhibit some kind of nest aggregation. Five nests were found within an area same area, with each nest separated by a distance of 200 – 300m.

4.0 Behavior study on *Hypotrigona gribodoi* in Cameroon with reference to the Process of Provisioning and Oviposition (POP)

4.1 Abstract

The oviposition behavior of *Hypotrigona gribodoi* was observed in Cameroon from May 2008 to November 2008. These bees are among the smallest bees found in the world. They are recognized under different local names depending on the clan or native language of the people. However, most people in the Bamenda highlands can recognize these bees as `nwauah`. A study on cell provisioning and oviposition process (POP) of these bees shows the following behavioral features:

1. The queen stays most of her life in the brood nets except during early stages of cell construction.
2. The brood cells are constructed in clusters and in a disorderly manner, without any particular plane at the surface to distinguish the newly constructed cells from the old ones.
3. They exhibit semisynchronous brood cell construction with exclusively batched queen oviposition.
4. The workers clean their nest during the early hours of the day and dump the dirt just below the nest entrance.
5. The coactions or interactions between the queen and the workers are mostly cordial. The queen feeds the worker in since instances.
6. The workers were never seen laying trophic eggs and only a single queen in the colony was observed throughout the research period.

Hypotrigona gribodoi are generally calm during manipulation. No case of attack on any body part was registered during the research period. However, these bees are capable of protecting their nests from other invading bees when their honey pots are damaged. This was observed with the presence of *Meliplebeia ogouensis* and Apis invading the hive to steal honey from ruptured honey pots.

During the oviposition phase, the queen suddenly becomes aggressive towards any worker bee found on already provisioned cell, by pushing and chasing the worker away from the surface of cell in order to stop the workers from laying egg. The queen in most cases succeeded in laying her egg into the covered cell after vigorously pushing the worker aside.

4.2 Introduction

The stingless bees together with the honeybees represent the most advanced stage of social differentiation in the Apidea. Some etho-sociological characters suggest that their equivalent social status was attained independently (SAKAGAMI 1982). In social groups which are less advanced, behavioral control of workers by queens seem frequent (WEST EBERHARD 1969; YOSHIKAWA et al. 1969).

Bees constructs cup-like structure (cells) in which larva food is poured into from the mouth of the workers. The process of spitting larva food into the cells is known as food provisioning. After the cells must have received enough lava food, the queen then lays her egg into the provisioned cell in the process known as oviposition.

The oviposition process of stingless bees proceeds with a complicated and highly group specific temporal sequence of queen-worker interactions. This behavior is unique to social insects (MICHENER 1974; SAKAGAMI 1982). But this kind of complex organization is shared by only two eusocial bee groups; the honeybees (Apinae) and the stingless bees (Meliponinae).

Taking the queen oviposition as a focus, the daily life of stingless bee colonies proceeds through an alternation of several phases, roughly divided into quiescent ($\overline{Q}$), transient ($\overline{T}$), patrolling ($\overline{P}$), arousal ($\bar{A}$), and oviposition phases ($\overline{O}$).

Each oviposition is further divided into several phases, basically formulated as Predischarge (r) + Discharge (d) + Oviposition (O) + Operculation (s).

In other words, cell construction (C), food provisioning (D), oviposition ($\bar{O}$) and cell operculation (S) form a tight link process, C.D.O.S., which passes during a short time under high excitement, often reinforced by peculiar behavior (SAKAGAMI & ZUCCHI 1974). This basic pattern receives modifications in each group of stingless bee according to their group specificity. In this study therefore, the ethological diagnosis of *Hypotrigona gribodoi* is given and the ethological features are compared with the oviposition process of some well studied taxa. Attempts are also made to analyze the peculiar behavior of this species and compared with that of related species.

4.3 Materials and methods

A survey of stingless bees was carried out in the Bamenda highlands of Cameroon in 2006-2007. Bee farmers practicing meliponiculture along side apiculture were used as informants for the search of stingless bee nests in the forests and farmlands. Hunters and ordinary farmers were also used to obtain information concerning the nests of stingless bees. *Hypotrigona gribodoi* often nest in trees and mostly in tree branches with cavity.

The tree branches found to be used by the bees was carefully cut down using a machete and a saw. The exact portion of the branch containing the nest was trimmed into a portable block of wood. The nest entrance was sealed with leaves and the whole colony transported by a car to Bamenda where observations were done. The distance between Maboua (original place of nest) and Bamenda (laboratory) is approximately 100km.

The colony was left untouched for a week to permit the bees regain their normal activities and get use to their new environment after distances resulting from transportation.

The tree block containing the nest was carefully excavated and the whole colony was removed and introduced into a Styrofoam observation hive with a transparent glass lid (see Fig. 72 below).

The glass lid was often covered with a dark piece of cloth when observation was not taking place. The dark cloth prevented direct light rays into the hive and kept the colony in its similar dark state as in the tree cavity.

Observations started in June 2008 and lasted till November 2008. The dimensions of the observation hive were as follows: 35cm x 24cm X 12cm. An artificial nest entrance was introduced to the observation hive using a silicone tube as shown below (Fig 73) At first, the worker and guard bees were skeptical of using the artificial entrance until some resin from the original nest entrance was smeared onto the silicone tube entrance.

The techniques we used for the rearing of *Hypotrigona gribodoi* was a modification from the methodologies of earlier studies done by LINDAUER & KERR (1958), NOGOUERIE-NETO (1964), WITTMANN et al (1991), SAKAGAMI & ZUCCHI (1971).

Observations were focused on the behaviors involved in the process of provisioning and oviposition. In order to have more reliable results several observations and 30 video recording sessions were made. Observations were made during the day and at nights when necessary. Behavior terminology we are adopting here is basically following that of Sakagami and ZUCCHI (1974) and SAKAGAMI (1982).

Figure 64. Colony of *Hypotrigona gribodoi* inside tree branch cavity

Figure 65. Observation hive with glass lid

Figure 66. Artificial nest entrance

Adapted nest entrance with exit tube smear with resin from the original nest entrance.

Bees hanging round the newly introduced entrance tube trying to find their way into

4.4 RESULTS

4.4.1 Behaviour of *Hypotrigona gribodoi*

In our attempts to rear four different species of stingless bees (namely: *Dactylurina staudingeri, Axestotrigona ferruginea, Meliplebeia becarri and Hypotrigona gribodoi*) in observation hives in Cameroon, *Hypotrigona gribodoi* was the most efficient is adapting to the local laboratory conditions.

During the observation period, bees were constantly manipulated but no case of guard bees attacking parts of the body was registered. However, an expression of defense behavior was observed with worker bees of *H gribodoi* clinched on the wings of other bees intruding into the hive to collect spilt honey from ruptured honey pots. *H gribodoi* guard bees will continuously bite the wings of the intruder until the intruder is rendered helpless.

The queens of other stingless bee species spend most time shuttling between the combs and the floor of the hives, sometimes on the glass lid except during the oviposition period (O) in most behavioural studies. But in *Hypotrigona gribodoi*, the queen turn to stay at particular areas in old brood cells and comes out regularly to visit the new cells under construction. Generally, she does not beat the wings when she is resting but she does beat the wings with intermittent strokes when she is walking or cruising. During queen resting, workers formed a royal court around the queen. Workers were seen coming towards the queen making forward and backward movements, sometimes touching the queen with their

Interaction between the queen and the workers of *Hypotrigona gribodoi* is very cordial and simple when they come in contact. An exception to this queen – worker coactions was observed in some four instances during the oviposition phase with the queen becoming aggressive to workers sitting on already provisioned cells and refusing to let the queen perform her egg laying task into that cell.

In some instances when the queen suddenly comes in contact with a worker, the worker escapes to the opposite direction or enters the nearby openings of old cells.

Contacts between the proboscis of queen and workers were frequent lasting between up to 90 seconds. Among 30 carefully observed buccal contacts, 4 cases actually resulted in food delivery from the queen to the worker instead and none from the worker to the queen.

Darting appears regularly on the newly oviposited cells when the queen comes in contact with a worker. After mutual contacts with the antennae, the worker rapidly raises her mandibles and antennae and dashes towards the queen, with forelegs extended and touching the queen´s face rapidly and the she retreats. Workers also used their antennae to touch the abdomen of the queen in royal court.

4.4.2 Cell construction

The type of cell construction manifested by *Hypotrigona gribodoi*, is semisynchronous (S_m) cell construction (i.e. construction of new cells starts successively but the difference between growth stages in the cells becomes gradually smaller).

Cells of *H. gribodoi* are constructed by successive activities of many workers. The task abandoned half way by a worker is taken over by another worker. The construction of new cells can occur at any place on the surface of the already oviposited cells of the cluster. The start of

construction of new cells is inhibited once the cells under construction attained an advance stage ready for provisioning (collard).

The process of larva food discharge and egg laying into individual cells of *Hypotrigona gribodoi* is exclusively batched (B_e). Food discharge and egg laying into many cells constitute a batch. Normally, exclusively batched means, all cells in the batch are food provisioned and eventually receive an egg each from the queen. In *Hypotrigona gribodoi* though, this was the case with some of the batches. A few collard cells were not provisioned and did not receive any egg from the queen during the oviposition process. As seen below (Table 9), the average number of cells found under unattended to by the queen after the oviposition phase (egg laying phase) in a batch were significantly low per batch (1.6 ± 1.02; n=22) with a range of 1-3 unprovisioned cells. However, in 8 of the 22 batches observed, only 1 cell each did not receive an egg and in 2 batches all the cells in the batch were provisioned with larva food and oviposited.

The batch size of *Hypotrigona gribodoi* ranged from 13 - 28 cells with a minimum of 2 batches per day and the mean number of cells per batch was 19.95 ± 5.02 cells, n= 22 (approximately 20cells per batch).

A mean oviposition rate of 5.47 cells per minute ($\bar{X}$ =5.47 ± 2.20 oviposition, n = 22).

The duration of the whole process of POP starting from the beginning of cell construction to end of oviposition ranged from 3.55 – 8.20 hours and the mean duration was 6:20 hours per POP. This can be summarized as follows: POP = Cell construction + Patrol phase + Oviposition Phase = 6 hours 20minutes (mean).

Table 9. Numerical data on the batch size and oviposition rate in *Hypotrigona gribodoi*.

Dates	Total Nr. Of cells in batch	Nr. Of cells oviposited	Nr. Of cells Not oviposited	Duration of O (Min:secs)	Duration of POP (H:m)	Approx nr of O per min
03.07.08	16	15	1	6:12		2.4
03.07.08	14	13	1	3:55	5:15	3.3
05.07.08	17	14	3	4:12		3.3
06.07.08	13	12	1	3:08	6:35	3.8
09.07.08	17	14	3	6:20		2.2
12.07.08	19	16	3	2:15		7.1
13.07.08	17	16	1	3:27	8:20	3.6
14.07.08	21	19	2	4:00	5:44	3.6
15.07.08	20	17	3	3:35	4:07	4.7
16.07.08	23	22	1	3:06		7.1
19.07.08	20	17	3	1:56		8.8
20.07.08	23	23	0	4:18	3:55	4.1
21.07.08	27	26	1	3:30	6:45	7.4
22.07.08	29	27	2	3:15		8.3
26.07.08	25	22	3	2:24		9.1
01.08.08	23	21	2	3:37		5.8
02.08.08	19	18	1	4:10	8:18	3.3

02.08.08	21	21	0	2:50	5:57	7.4
04.08.08	31	29	2	3:15		8.9
05.08.08	26	25	1	3:44	5:26	6.9
06.08.08	26	24	2	5:10	8:14	4.6
09.08.08	28	28	0	4:32		4.7
MEAN		19.95	1.63		6:20	5.47
STD		5.02	1.02			2.20

4.4.3 Behavior before food discharge in brood cells

After each oviposition (end of operculation), the queen leaves the top surface clusters to her resting place which is usually underneath the cell cluster. She comes out from time to time to visits the cell cluster, cruises around checking the new cells under construction and then returns to her resting place.

One or two workers can be seen attending to the new cells, inserting their body into the cell. In some cases, worker body insertions into cells can last for more than 30seconds.

When the queen arrives at a cell (queen patrol), the workers gently avoid her by just inclining their body upwards. She stays by the cell for a while, either hanging on the cell or sitting on a neighboring cell, and then leaves the cluster after walking around the cell.

The number of workers attending the cells increases and the duration of each body insertion shortens. The alternation between the workers attending to the cell and workers body insertion becomes more and more frequent, indicating that the beginning of the next phase (larva food discharge or cell provisioning phase) is soon starting. Usually, it is complex to draw a clear line between the two phases.

Queen patrolling becomes more frequently as the cells under construction progresses in height. The more closely the cell become ready to be food provisioned, the more frequent the queen patrols on the cluster surface of the cells.

The behavior in the patrolling phase in other taxa as well as in *Hypotrigona gribodoi* is usually characterized by the following key features;

1) Appearance of collard cell or completed but unprovisioned cells.
2) Congestion of workers in the brood cell area and
3) Increased and prolonged queen visits to the brood area.

These features are quite distinct with *Hypotrigona gribodoi* as seen in table 10 below. During the early part of the patrolling phase, the queen visits to the brood cell cluster is less frequent with the duration of each visit on the cell surface ranging from as low as 1second to up to 58seconds stay. The mean duration of queen stay of the cell surface however was: 32.5 ± 10.8 seconds, n=11.

In eleven observed cases, the number of visits registered ranged from 8 to 20 visits per case, with a mean number of visits: 13.4 ± 3.4 visits; n=11.

The duration of the whole patrolling phase was measured in 11 cases and the mean duration of the phase was: 80.6 ± 18.1 minutes; n=11.

Table 10. Some numerical data on queen behaviour related to Patrolling phase (P)

($\overline{P}$)case nr	Nr of queen visits during P phase	Average duration of queen visits (secs) in P	Duration of P (mins)
1	15	24.13	74
2	11	33.3	57
3	12	25.25	66
4	16	31.18	89
5	9	32.22	123
6	12	45.08	67
7	14	21.14	73
8	20	58.1	64
9	8	40	98
10	17	26	90
11	13	21.38	86
Mean	13.36	32.52	80.63
SD	3.36	10.82	18.14

During this patrolling phase, the behavior of both the queen and workers are quite simple and cordial. When the queen is visiting cells, she stays on already oviposited cells, touching the brim of the cells with her antennae and she inspects the cells occasionally by inserting her head into the cells for a while.

One or two workers attend to each of the cells where the queen stops during her patrol. The general behavior of the queen does not change during this phase. Workers gradually accelerate the repeated head and metasomal insertions into the cells some times with or without change of individuals.

The duration of workers body duration insertions in to the cells could last for up to 74seconds. When the queen arrives at a cell, the worker attendants to the cell immediately abandon the cell after attempting to make body insertion into the cells.

During the patrolling, the queen spends much more of her time cruising (walking) on the cell clusters rather than staying at a particular cell. The workers who accidentally come in contact with the queen when making body insertions, quickly withdraws from the cell and escape into nearby openings or nearby cells. Some workers will turn around and move away to the opposite direction.

4.4.4 Behaviour of bees during arousal phase

The start of the arousal phase (Ā) is marked by a distinct increase in the agitation displayed by both queen and worker attendants. Congestion of workers at the brood cell area becomes even more compared to that of the patrolling phase. The behavior during the arousal phase does not differ much from those seen in patrol phase.

Generally, the coaction between the queen and the worker is equally simple without any form of rituals. During the later parts of the patrolling phase and the arousal phase, queen-worker interactions are much simplified and are predominantly represented by queen inspection and worker body insertions with fewer pushing and darting.

The queen walking rhythm gains considerable speed and agitation during arousal, and her wing movements tend to vibrate more continuously than in the patrol phase. Her cruising on the cluster is gradually replaced by brief visits to some collard cells.

The excitement that the queen arouses at each cell sometimes culminated in a high excitement over the cell cluster but sometimes the excitement is limited to particular areas on the cell cluster.

4.4.5 Behavior of bees during queen Predischarge waiting

Table 11. Numerical data on the arousal ($\bar{A}$) and predischarge behavior ($\bar{r}$)

Nr of prolonged queen waiting (W) in $\bar{A}$	Nr of queen inspection during $\bar{A}$ (E)	Nr of queen inspection during $\bar{r}$ 1 (e)	Nr. Of workers insertion during $\bar{A}$	Nr. Of workers insertion during $\bar{A}$
0	3	1	3	5
0	4	2	3	11
1	3	1	2	7
0	2	1	3	5
0	4	1	1	2
1	1	0	1	6
1	3	0	0	7
0	2	1	0	8
0	4	1	2	2
0	2	1	2	1
0	1	3	1	3
0	4	1	0	1
1	3	1	0	1
0	1	2	1	4
2	2	1	2	8
Mean ---- 0.4	**2.6**	**1.1**	**1.4**	**4.7**

This phase is marked by the queen arrival at the first cell to the first food discharge by the worker into a cell. As in many taxa, when most cells are structurally completed (collared cells), they engineer an excitement gathering of workers on the surface of the cluster. The workers alternately insert their fore bodies into the cell indicating to the queen their intentions to deliver larva food discharge act into the cells.

In *Hypotrigona gribodoi*, the appearance of the excitement was very conspicuous. The behavior of both workers and queen was very simple in this phase. In both the arousal and the predischarge phase, queen inspection and workers body insertion into cells was not ritualized.

The cells that were first provisioned and oviposited were not necessarily the first cells by which the queen waited in predischarge phase and were not necessarily followed by food discharge and queen oviposition in the same cell.

In 25 carefully observed cases, none of cells where the queen waited was followed by food provision and eventual oviposition in same cell.

The duration of the Predischarge phase ($\bar{r}$) range from 85-105seconds (mean 77.75 ±17.78 seconds; n =12). See Table 12 below.

Among 15 observations of the predischarge waiting phase, queen inspection was noted in 13 cases (see table 11 above).

Generally, the time spent by the queen on cruising is much longer than the time she spends making prolonged waiting during the arousal phase (table 11). Prolong waiting here means the queen stopping for more than two seconds at a particular cell during this phase.

The queen performs relatively fewer cell inspections in the Predischarge phase than in the arousal phase (table 11 above).

The number of worker insertions in to the collard cells during the Predischarge phase is almost trice as much as that in the arousal phase as seen in table 11 above.

4.4.6 Behaviour during food discharge phase

Finally, after several rapid body insertions, a worker discharges the first droplet of larval food from the mouth into a cell. The cell where the first food discharge takes place never coincided with the cell where the queen predischarge waiting (¯r) took place. All the collard cells are food provisioned with larva food successively by many workers. This happens after the alternation of agitated insertions by many workers and some workers contract their metasoma and discharge the larva food into the cell. After a worker makes her discharge, she quickly retreats and leaves

the cell making way for the next worker to make the next discharge. This is behavior is repeated for all the collard cells in the batch ready to be provisioned.

After a cell receives sufficient food, a worker stays on the margins of the cell, checking the cell rim with the antennae but do performs neither body insertion nor removal. The congestion of workers around a cell undergoing provisioning gradually clears out as soon as the cell is filled with larval food, making the approach of the queen possible. Usually, just one worker take control of the cells with sufficient food and protects filled cells from any further discharges. The discharges are done successively i.e. one worker before the next.

Intentional body insertions by workers are seen before the arousal and predischarge phases are replaced by actual ones when the queen arrives and stays at a particular cell.

After each food discharge, the worker slightly withdraws herself towards the lower part of the cell. The first discharge is immediately followed by the second and subsequent discharges. The mean number of discharges per cell was very high, 34.2 ± 5.9; n=37.

The duration of each discharge is short, mostly one second or slightly higher (1.10 ± 0.38 seconds; n=37). In 37 cases observed: 1 second (29cases), 2seconds (7cases) and 3 seconds (1case).

Postdischarge subphase (the time between the final discharge and the beginning of cell inspection by the queen) is very short and simple and virtually absent in most cases recorded. No specific measurements were taken during this phase because of it inconspicuousness.

4.4.7 Queen Oviposition and Operculation

The queen lays her egg immediately (Oviposition) following a brief cell inspection period which usually lasted under a minute. The duration of queen oviposition time (egg laying into a cell) ranged between 2-7seconds with a mean duration of ($\bar{X}$ = 3.75 ± 1.11 seconds; n=111).
The interval between 2 oviposition was between 5-14 seconds with a mean interval of ($\bar{X}$ =8.4 ± 2.8 seconds, n=16). The queen beats her wings more or less continuously while laying egg.

The duration of a complete queen oviposition into all collard provisioned cells ranged from 6.25 to 12.1 minutes, with a mean duration of 8.75 ± 2.23 minutes; n = 12 (See table 12 below)

An interesting queen behavior was observed in 4 instances during the oviposition phase was observed during the study period with some 4 workers refused to allow the queen assess to lay her eggs into already provisioned cells. This resulted into a fight between the queen and the worker at the brim of the cell. At the end, the queen gave up the fight and concentrated on the other provisioned cells. This behavior lasted 10seconds (1case), 12(1case), 15(2cases). The workers did not lay any egg in any of the cases.

After the final oviposition, the queen often stays on the cell clusters and visits the different cells under operculation (sealing of cell) by the various workers. During these visits, workers do not

show any signs of aggressiveness or reaction to the queen advances. Coaction between workers and the queen is simple in this phase.

Cell operculation ($\bar{S}$) starts immediately after queen oviposition. Soon after the queen oviposition ends, a worker sits on the brim of ovposited cell, inserts her metasomal tip into the cell and work by rotating herself on the cell.

The mean duration of the operculation for a single cell ($\bar{S}$) range from 313 – 780 seconds ($\bar{X}$ = 484.5± 112.3, n=48). Meanwhile the mean duration of the operculation phase ranged between 455 and 815seconds ($\bar{X}$ = 646.8 ± 64.4 seconds, n = 12).

The rotation sub phase ($\bar{S}_r$), took more than 75% of the total duration. Meanwhile the $\bar{S}_t$ subphase was not actually noticed in Hypotrigona. The sidework ($\bar{S}_s$) subphase lasted just a few seconds and not very clear for measurements. Change of operculator was never observed during our observation period.

Table 12. Duration of oviposition in some accurately measured cases (seconds)

total duration of POP							
cases	# of cells	Arousal	Predischarge	Discharge	Oviposition	Operculation	Total O phase
1	11	75	85	160	420	650	1390
2	13	87	74	95	450	630	1336
3	13	85	60	90	375	675	1285
4	14	97	57	180	435	780	1549
5	14	76	94		459	640	1269
6	15	198	77	105	730	815	1925
7	17	132	105	145	366	455	1203
8	17	165	66	75	720	620	1646
9	20	207	89	65	570	590	1521
10	20		45	133	725	710	1613
11	21	208	78	133	525		944
12	23	235	103	120		550	1008
Mean		142.27	77.75	118.27	525	646.81	
SD		47.69	17.78	28.53	136.72	68.46	

The total duration of oviposition process is define here as the A (arousal phase) + $\overline{r}$ (Predischarge subphase) + $\overline{d}_p$(discharge subphase) + $\overline{O}$ (oviposition phase) + $\overline{S}$ (operculation phase) was measured in 12 cases as in Table 12.

Comparing the above results with that of other studied genera shows that Hypotrigona gribodoi manifest peculiar differences as well as similarities with other well studied taxa.

4.5 Discussion

Behavioural characteristics of *Hypotrigona gribodoi*

The oviposition process of *Hypotrigona gribodoi*, studied in Cameroon proceeds with distinct phase sequence as in other stingless bees studied so far. Further, there are several ethological characteristics common to the other groups that are also shared by *Hypotrigona gribodoi*. These characteristics are:

1. Rapid succession of food discharges by workers into cells
2. Rapid escapes of workers from the cell following food discharge
3. Increased in workers body insertions during the patrolling and arousal phase
4. Worker-queen relation showed repetition of pushing followed by a retreat by attendants in front of the queen, workers avoiding approaching queen and formation of royal courts around resting queen
5. Queen lays egg vertically on larva food
6. Cells are constructed by several workers successively as in honeybees, not through the work of a single worker as in bumble bees
7. Oviposition process can be divided into successive stages and phases which is not the case with other social insects
8. Absence of workers licking the queen
9. Rarity of food delivery by workers to the queen

A detail comparison of the ethological features of *Hypotrigona gribodoi* with those of other closely studied taxa is given below with special reference to the queen- worker coactions and oviposition process. All species listed here are South American species. The groups compared with are abbreviated as follows:

Table 13. Scientific names and abbreviations of some stingless bees

Scientific names	**Abbreviations**
Leurotrigona mulleri	Lt
Trigonisca duckei	Ts
Mourella caerulea	Mr
Cephalotrigona femorata	Ct
Tetragona clavipes	Tt
Scaptotrigona postica	St
Melipona compressipes	M
Duckeola ghillianii	D
Friesella	F
Nannotrigona testaceicornis	Nt
Lepidotrigona ventralis	Lp

The arrangement of cells in clusters as found in *Hypotrigona gribodoi* is similar to that of Lt, Ts, Tt and neither complete combs as in Lp, M,Ct, Tt,Mr,St, Nt, nor semi combs as in D and F.

1. The absence of involucrum is similar to D, Lt, F,Ts but different from St, M, Mr, Ct, Tt.
2. Differentiation of honey and pollen pots absence is similar to St, Tt, M, Lt, D,F,Ts, Ct
3. Cells and pots are semitransparent as in Lt, Ts and not opaque as in Nr
4. Waste materials are dumped down at the nest entrance similar to Ts , Lt, not carried away on the wings as in St, M, Ct, Tt, D, F, Mr, Nr
5. The nest is never subterranean similar to all other taxa but different from Mr
6. Cell construction is Semisynchronous (S_m), similar to D, F, Ts, not synchronous (S_y) , as in Lt, or successive (S_c) as in St, M, Ct
7. Cell construction is not started by accumulation of large amount of cerumen as in D but similar to St, M, Tt,F, Ts, Lt

8. Queen walks with moderate speed same as in M, Ct, Tt, Lt, F, Ts not slowly as in Nt, St, D

9. Rhythmic wing movements of queen present being vibration similar to Lt, D, Tt, F not single strokes.

10. Food discharge in cells is successive, Ds, different from St, but same as in Nt,M, C,Lt, D, F, Ts

11. Queen more cruising than waiting by a particular cell during patrolling and arousal phase similar to Lt but different from most groups

12. Excitement arousal is localized similar to most group but different from St

13. Worker excitement before food discharge is conspicuous different from D, F but similar to all other groups.

14. Queen cell inspection in arousal and discharge phase is rare similar to F, Ts, Lt but different from more frequent inspection in St, Nt, M

15. Queen not violently tapping workers attending cells similar to St, Lt, Tt, D but different from M, F, Ts, Nt, Mr

16. Workers body insertions before food discharge are rare similar to F, Lt, but different from M, Nt, Ct, St, D, mostly replaced by intentional insertions

17. Number of food discharge per cell is very high different from all other groups.

18. Post discharge sub phase virtually absent similar to F,D, Ts, Lt but different from St, M, Ct, Tt

19. Metasoma contraction at food discharge is conspicuous

20. Worker body insertion at each food discharge is very short

21. Before food discharge worker behavior is simple without ritualized responses similar to Ct, D, M, Lt, Tt but different from F, St, Ts

22. Worker oviposition during oviposition process is absent similar to Lt, D, F, Ts but different from St, M, Ct, Tt, Mr, Nt

23. Queen oviposition moderately long similar to D, Nr, St, Ts, Tt

24. Queen oviposition made with peculiar leg twitching similar to D
25. Cell operculation starting without any delay similar to St, Lt, Ct, D, F, Ts, but different from Tt
26. The rotation($\overline{S}_r$) and sidework ($\overline{S}_s$) sub phases are well differentiated without the intervention of the transient subphase($\overline{S}_t$), similar to Lt, St, M, but different from Ct, Tt, D, Ts, F,
27. The duration of operculation is moderately long similar to St, M, Ct, D, F, Lt, Mr, Nt, but different from Tt, Ts

Obviously some of the above mentioned features may vary according to colony conditions and seasons. However, many of these characters, if not all could be seen as characteristics of *Hypotrigona gribodoi*.

Hypotrigona gribodoi is peculiar by its simple and easy behavior with no exaggerated or ritualized behavioral patterns and extreme excitement level during oviposition. From the above ethological diagnoses, the number of character states shared (n_1) or not (n_2) with *Hypotrigaona gribodoi* are given below for each taxa as n_1 / n_2 following the descending orders of n_1:

Leurotrigona 17/2 > Duckeola 13/9 > Trigonisca 12/5 > Friesella 11/7 > Tetragona 10/10 > Scaptotrigona 7/13 > Melipona 6/8 > Cephalotrigona 6/9 > Lepidotrigona 0/4 > Nanotrigona3/9 > Mourella 2/7.

The above character states represents a preliminary attempt towards phylogenetic and other comparative analyses in view of increasing the number of studied taxa and establishing a the phylogenetic polarities of each character.

The above results show that *Hypotrigona gribodoi*, shares most ethological features with Leurotrigona, Duckeola, Trigonisca and Tetragona. Aside Duckeola which is a semi comb maker in the list of most shared characters with *H. gribodoi*, all the others (Tetragona, Leurotrigona and Trigonisca) are cluster makers like *H. gribodoi*. The least character states shared was with Mourella and Lepidotrigona. None the less, *H. gribodoi* is peculiar in the following characters when compared to the others in the most shared characters:

- The number of food discharge per cell is exaggerated
- Queen oviposition is made with leg twitching and
- The oviposition duration is longer than that of most studied taxa.

Colony condition can not be over looked at as a possible reason for the differences in some of the shared characters mentioned above. If not all could be characteristics of *H. gridodoi*.

A closer comparison between *H. gribodoi* and *Leurotrigona mulleri* and *Hypotrigona duckei* is shown in table 14 below. Behavioral characters common to the three groups are as follows:

- Cells are arranged in clusters.
- Involucrum is absent.
- Differentiation of honey and pollen pots is absent.
- Waste materials are thrown down from the nest entrance.
- Queen – worker exaggerated interactions out of oviposition process is absent.
- Queen walking with moderate speed.
- During food discharge queen continuous to wait at a particular cell.
- Food discharges in cells is successive
- Queen cell inspection in arousal and discharge phases rare
- Worker oviposition is completely absent.
- Queen oviposition relatively short.
- Cell operculation started without much delay.

Some characteristics common exclusively to *H. gribodoi* are as follows:

- ✓ The extremely high number of discharges per cell
- ✓ Wing beats during rest and at walks at times though not continuous
- ✓ Oviposition pattern is exclusively batched but 1-3 collared cells were left unprovisioned in some batches.

Table 14. Behavioural differences between *L. mulleri*, *H. duckei* and *H.gribodoi*

	Characteristics	*Leurotrigona mulleri*	*Hypotrigona (Trigonisca) duckei*	*Hypotrigona gribodoi*
1	Rhythmic wing movement of queen	Relatively rare but present at walk	Extremely rare	Present at walk and during rest sometimes
2	Cell construction	Synchronous (S_y)	*Semisynchronous (S_m)	Semisynchronous (S_m)
3	Excitement at cell construction	*Relatively high	**Not conspicuous	inconspicuous
4	Oviposition pattern	Exclusively batched (B_e)	*Singular (B_e) in the colony observed, probably facultatively batched (B_f) under favorable conditions	Exclusively batched (B_e)
5	Pattern of Predischarge queen behavior	More cruising than waiting (CW)	More waiting than cruising (cW)	More cruising than waiting (CW)
6	Shortening of secondary Predischarge waiting	Inconspicuous	*Occasionally conspicuous	*Inconspicuous
7	Predischarge worker behavior	Simple, body insertions into cell replaced by intentional ones at queen waiting	Intentional insertions rare. Peculiar behavior, presentation of metasoma to queen prevailing	Simple, body insertions into cell replaced by intentional ones at queen waiting

8	Predischarge queen behavior	Simple, waiting short	Waiting long with violent beating of workers with antennae and fore legs	Long waiting and simple
9	Number of discharges per cell	Low, mostly 2	Normal, 4~6	Extremely high, 30~47
10	Postdischarge escape	Inconspicuous	Distinct	Inconspicuous
11	Duration of operculation	Normal	Extremely long especially at the rotation subphase	Extremely long
12	Differentiation of rotation and side work subphases	Distinct	Indistinct due to persistence of rotation	Distinct

N.B. Studies on *Leurotrigonica mulleri* and *Trigonisca duckei* was done by SAKAGAMI & ZUCCHI (1974).

*= Characters that might require further confirmation

4.6 Conclusion

Hypotrigona gribodoi are generally calm with a single queen at any given time in a colony. Brood cells are constructed semisynchronously and the oviposition pattern is exclusively batched. Cell provisioning is done by extremely large number of workers and the duration of oviposition is longer than that of most stingless bees already studied. A close comparison with nearest relatives of H. gribodoi, shows that the queen feeds the workers in most cases instead of the workers feeding the queen as is the case with the others. Workers oviposition does not seem to occur in this species.

5 TASKS PARTITIONING AMONG WORKERS OF *MELIPLEBEIA BECARRI*

5.1 Abstract

Some tasks performed by workers of *Meliplebeia becarri* were examined in Cameroon to make ascertain the temporal task sequence compared to other stingless bees. *M. becarri* are monogynous subterranean stingless bees' species with an average life span of 52.7 days. Results from individually marked worker bees of *M. becarri* indicated that workers perform tasks according to age group. However, the main activities investigated, exhibited overlapping in the following sequence: Cerumen works, cell construction and cleaning of the nest. This aspect is more or less similar to that of other stingless bees already studied. Tasks related to nest reconstruction were started by very young workers and could last till when they are four weeks old. While tasks related to foraging were mostly done by workers at the later part of their life span. More than 50% of *Meliplebeia becarri* survived the first 50 days of their life span with lower mortality rate.

5.2 Introduction

One of the major features of eusocial insect species is the division of labour among the colony members. Division of labour refers to how the various tasks or duties in a colony of bees are being performed by the different members within a stingless bee society.

Eusocial bee societies are composed of only two morphologically distinct castes; the queen and the workers, unlike in other eusocial insects with more castes division like ants and termites. The principal function of the queen in a eusocial bee society is to lay eggs while the workers take up the rest of the tasks related to the survival of the colony.

In stingless bees, the workers exhibit considerable flexibility in task allocation: Tasks are not rigidly established but depend on the state of wax glands, food glands and the condition of the colony (SAKAGAMI 1982).

In a colony, workers can perform several tasks ranging from nursing of young bees to foraging.

Stingless bees like the other social insects live in colonies with castes differentiations. Morphological differentiation and division of labour characterize their social structure with an overlap in generations.

Among the workers, secondary division of labour do exists. Workers are distributed over the different tasks associated with their ages, although there is a high plasticity in this temporal distribution. Workers pass through age castes at different rates and individual differences occurs in the way certain tasks are predisposed. This is called age polyethism, which is influenced by colony condition, as in honey bees (GORDON 1996).

According to SAKAGAMI (1982), a typical labour division in eusocial bees proceeds with the following sequence: callow, nursing, household, and foraging. But the age related trend in the activities is very flexible, implying that the task sequence can be adjusted according to the colony condition. Our study therefore is to verify and confirm this trend with *Meliplebeia becarri* in Cameroon.

For the purpose of this study 9 tasks were retained to check the activity pattern and life span associated with the different age group of the workers of *Meliplebeia ogouensis*. The tasks are:

1) Cerumen works 2) Construction of cells 3)Reconstruction of involucrum, 4) Construction of pillars 5) Guarding the nest 6) Collection of pollen 7) Fanning the nest, 8) Collection of resin entrance and 9) Cleaning of nest.

5.3 Materials and methods

Throughout the research period, *M. becarri* was only found in Takijah village in the North West province of Cameroon. For the purpose of this study, 3 colonies were transported by car from Takijah village to Bamenda where observations were done. To ensure complete safety and the presence of the queen bee in the transported colonies, the whole colonies were dung out and placed in a bucket chucked with soil and plant materials inside the container (see figure below) protecting the colony from bumping onto the walls of the container. The whole colony was later introduced into an observation box made purposely for the study. An artificial nest entrance using a tube was assigned on the upper surface of the observation box through the transparent glass lid.

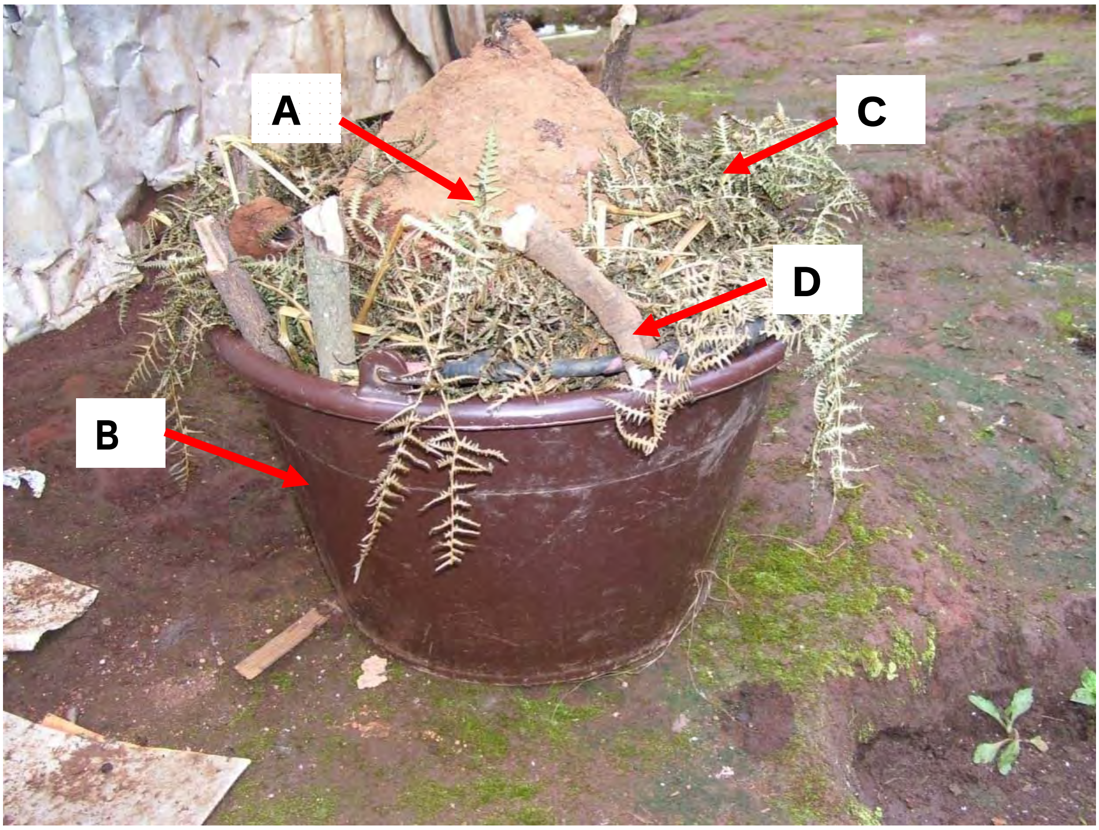


Figure 67. Bucket container with the full nest of *M. becarri* ready to be transported

A= soil mount with colony of *M. becarri*

B= bucket container

C= grasses to prevent bumping of nest to walls of container

D= pegs to protect soil and colony from breaking apart

Figure 68. Observation box with *M. becarri* colony inside

The study which lasted from July to November 2008 had as objective to find out the life span of the workers and to study the temporal pattern of task allocation by the workers.

Mature brood combs ready to hatch were taken out into a locally made Petri dish where new emerging worker bees were marked with distinguishing colours accordingly. For each batch, 15 bees were marked and introduced into the observation hive 30 minutes later. A total of 90 day old workers from the 6 different batches were marked.

The activities of the marked workers were observed for a period 3 hours daily. Data were collected throughout the life of the individual marked bees on specially designed collection sheet. Due to instability and frequent manipulation of the colonies, the following activities performed by the workers were retained according to the following description:

1. Working on cerumen – working on the old cells
2. Cell construction- working inside or on the brim of the cell under construction
3. Reconstruction of involucrum – workers found on the involucrum closing it

4. Construction of pillars – workers working on pillars both inside and outside

5. Collecting resin – workers bring resin into the nest
6. Collecting pollen – workers bringing pollen into the nest
7. Fanning nest – beating of wings
8. Guarding nest entrance – marked workers found at the artificial entrance into the nest
9. Nest cleaning – workers seen holding materials with mandibles

Activities related to the process of provisioning and oviposition could not be recorded because of the workers continuously sealed their brood area with involucrum after each manipulation, though in a few instances we managed to record activity on cell construction. A count of marked bees was done early everyday and any shortage or reduction in the total counts of the marked bees was noted as dead bees accordingly.

5.4 Results

5.4.1 Life span of workers of *Meliplebeia becarri*

Table 15. Life span of marked workers of *Meliplebeia becarri* (days)

Colony 1			Colony 2		
Batch 1	Batch 2	Batch3	Batch4	Batch 5	Batch6
68	73	64	70	71	66

Table 15, above shows data collected from the marked bees following their days of disappearance or death. Numbers represents the last days the oldest marked bee was seen in observation hive.

Table 16. Percentages of survival and deads of marked workers of *M. becarri*

Age (days)	Number of Dead workers	% of Dead workers	Number of Survived workers	% of Survivals
1 - 10	0	0	90	100
11 - 20	0	0	90	100
21 - 30	1	1.11	89	98.88
31 - 40	18	20	71	78.88
41 - 50	16	17.77	55	61.11
51 - 60	27	30	28	31.11
61 - 70	25	27.77	3	3.33
71 - 80	3	3.33	0	0

The cumulative table comprises both the survival and the dead rates of the marked bees projected in percentages. It covers the totality of all the different batches of the investigation during the observation period. Workers ages are grouped into 8 groups (table 16).

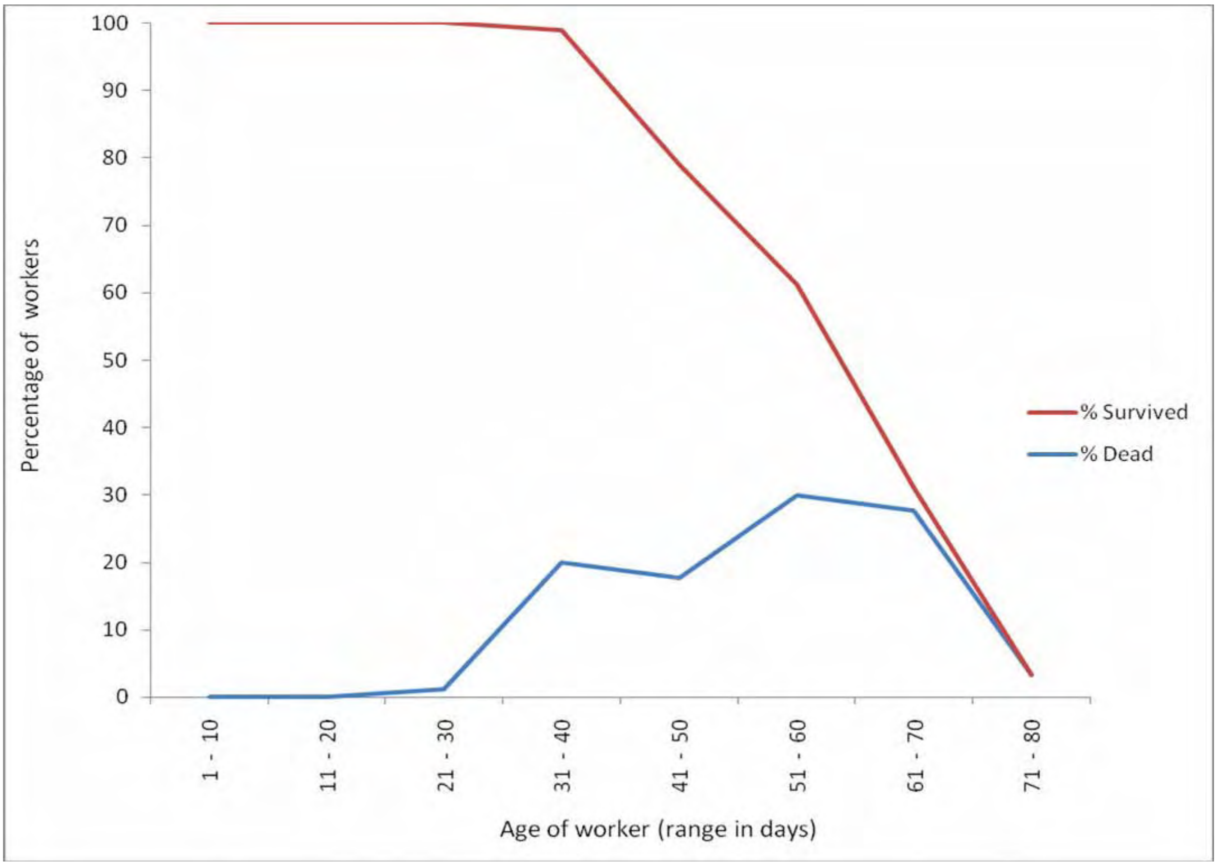


Figure 69. Curve showing the dead and survival rates for marked workers of *M. becarri*

The survival of the colony is relatively stable for the early days of the lives of the workers in *M becarri.* During the first 23 days, all workers were recorded in full performances in all the batches. Most of the workers bees would survive the early days of their lives with just about 21.1 % mortality in the first 40 days and 30 % in the last 10 days. However, most of the workers perished between the 40^{th} and 60^{th} days of the life with 47.7% .Generally, the first 23 days registered zero mortality for all the 6 batches meanwhile many more dead were noted after the average life expectancy of the workers bees (52.7 day).

Table 17. Average duration (days) spent for each task and average frequency of surviving workers involved in each tasks

	Number of Days							
Tasks	Batch 1	Batch 2	Batch 3	Batch 4	Batch 5	Batch 6	Average duration (days)	Average frequency of surviving workers (%)
Cerumen works	30	30	33	28	34	27	17.83	19.54
Cell construction	4	1	5	0	0	5	2.5	1.76
Working on Involucrum	27	26	29	25	31	29	18.83	28.24
Pillar construction	29	28	28	30	31	33	20.5	26.22
Collecting resin	36	28	33	33	32	35	17.33	34.44
Collecting pollen	36	29	28	37	31	26	17.16	21.01
Fanning nest	7	6	8	0	6	7	5.66	6.25
Guarding nest entrance	17	10	6	2	9	4	7.66	38.13
Cleaning nest	6	12	0	7	3	2	5	4.94

5.4.2 Task organization

5.4.2.1 Cerumen works

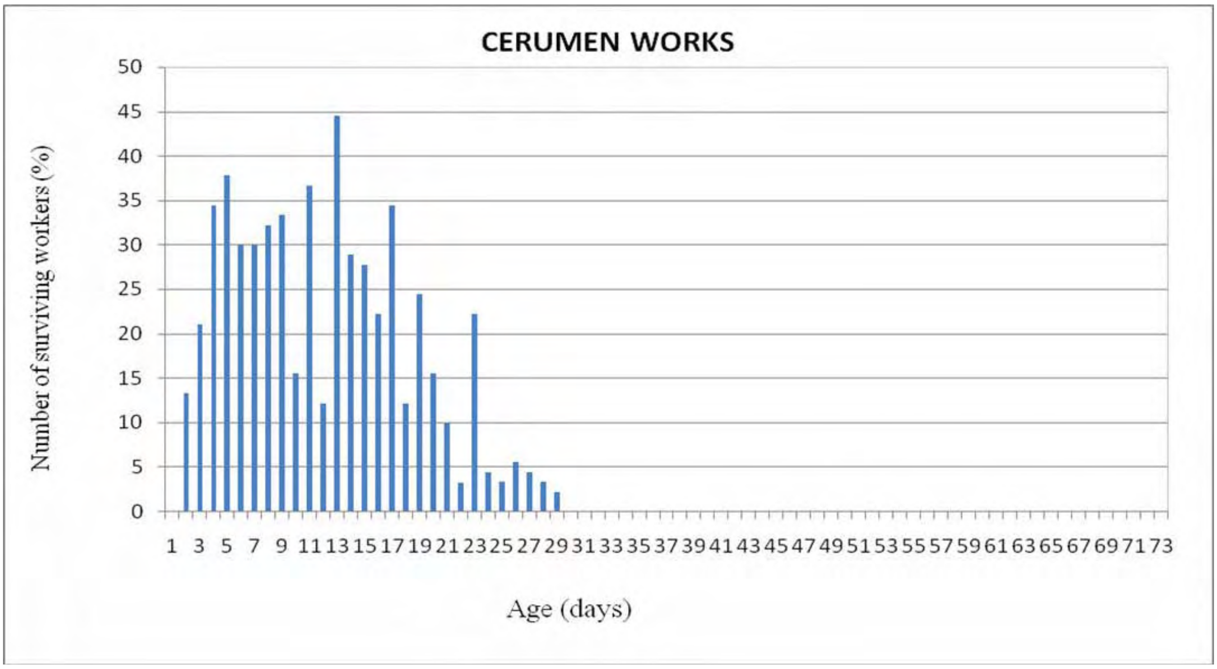


Figure 70. Frequency of workers of *Meleplebeia becarri* involved in cerumen works.

Workers commence their task on the cerumen immediately they are hatched and continue working until the 29th day of their life span. No worker was seen performing this task after the first 29th days. The average duration of this task was 18.73days. A maximum of 44 % of the total number of young workers in the colony performed this task with an average of 19.5% performance frequency of surviving workers of workers involved in cerumen reconstruction works. However, the frequency of the workers was unevenly distributed throughout their task period (table 17).

5.4.2.2 Cell construction

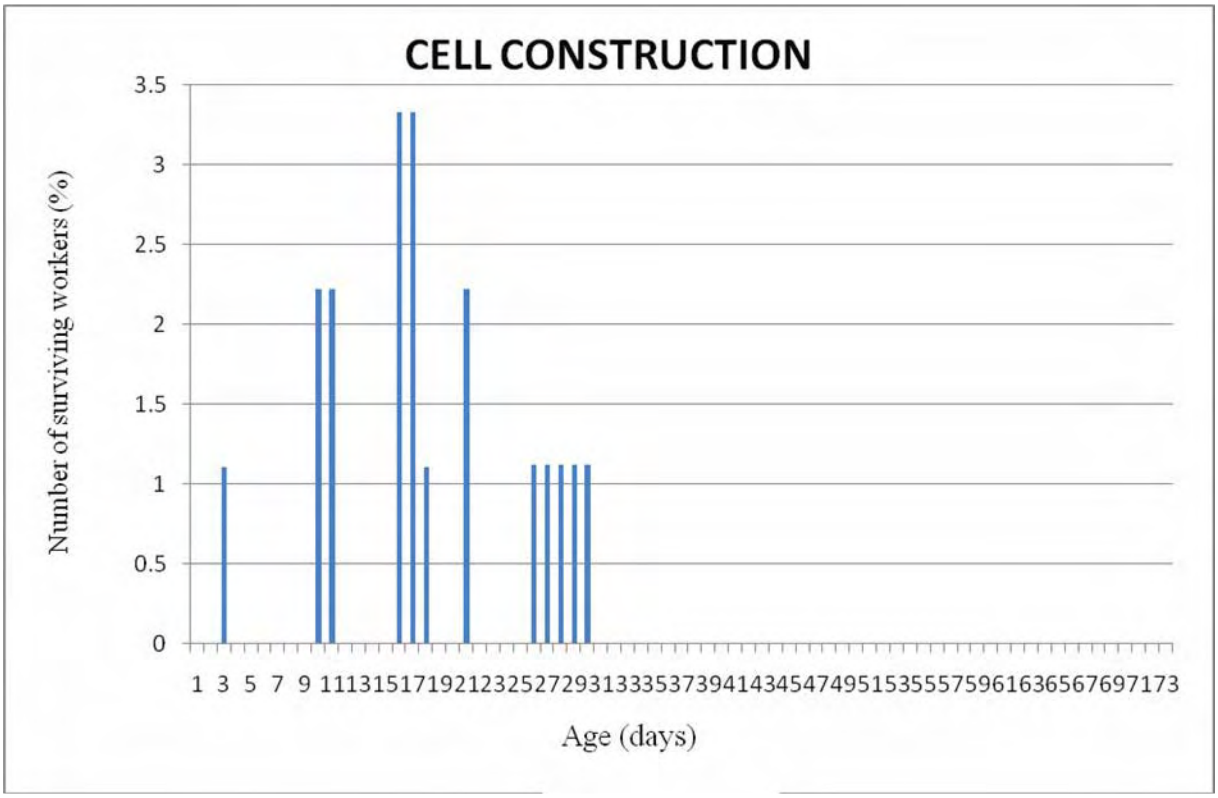


Figure 71. Frequency of *M. becarri* workers engaged in cell construction task

This task was poorly observed because of the condition of the colony. The highest record on this task was recorded by 3.3% of workers and the lowest was by 1.1% of bees. Under normal circumstances, it would have been much higher if we were able to take precise records during the process of provisioning and oviposition. Tasks related to this brood production was completely left out because, workers would not perform the related tasks with exposed combs (involucrum removed).

5.4.2.3 Involucrum works

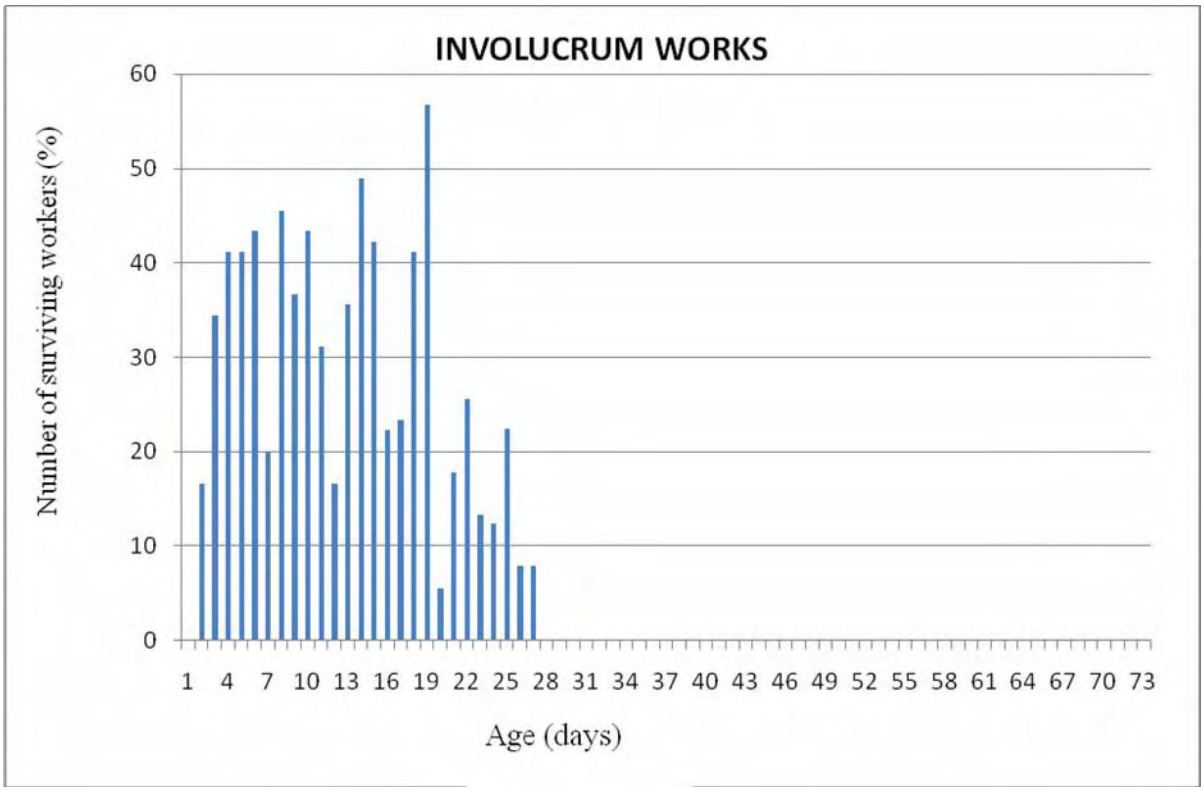


Figure 72. Frequency of workers of *M. becarri* engaged in construction of involucrum.

The average frequency of workers involved in reconstruction of involucrum was 28.2% of the surviving workers and the average period was 18.8 days (Table 17). The maximum number of workers that performed the task was 56.5% within the age of 19days while the lowest registered for this activity was about 5.5% of the workers. Construction of involucrum was done by workers of age 2-27 days old. Workers older than 27days never performed this task.

5.4.2.4 Pillar construction

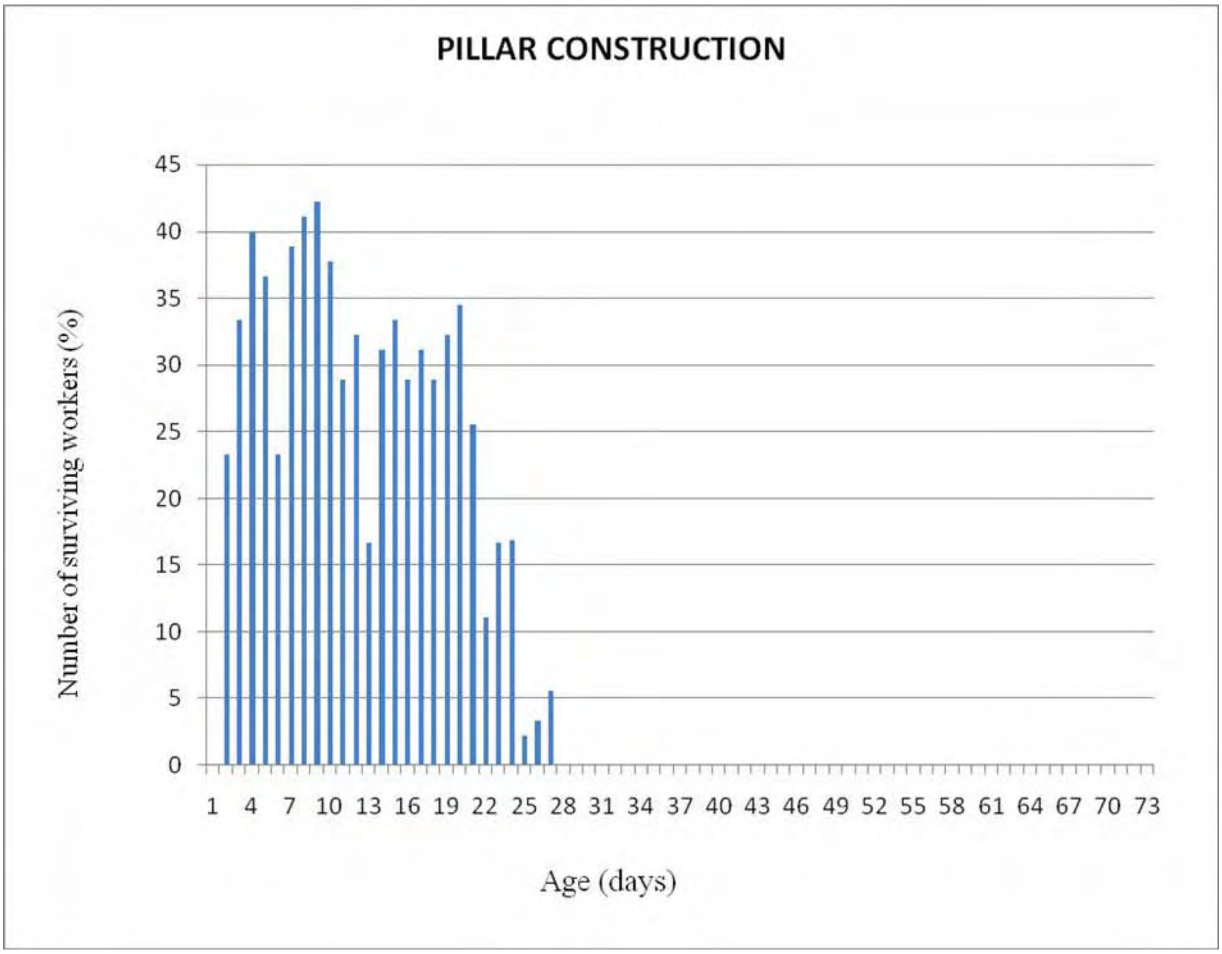


Figure 73. Frequency of workers of *M. becarri* engaged in construction of pillars.

On the average, pillar construction lasted 20.5 days with activity done by workers of 1- 28 days old. However, not all the workers of this age group took part in the activity. Averagely, 26.2 % of the surviving workers took active part in pillar construction with a maximum frequency of 42.2% workers participation at the age of 10 days. The minimum frequency of workers taking part was about 3.3 % of surviving workers. The activity was not however performed by workers older than 28days in any instance.

5.4.2.5 Resin collection

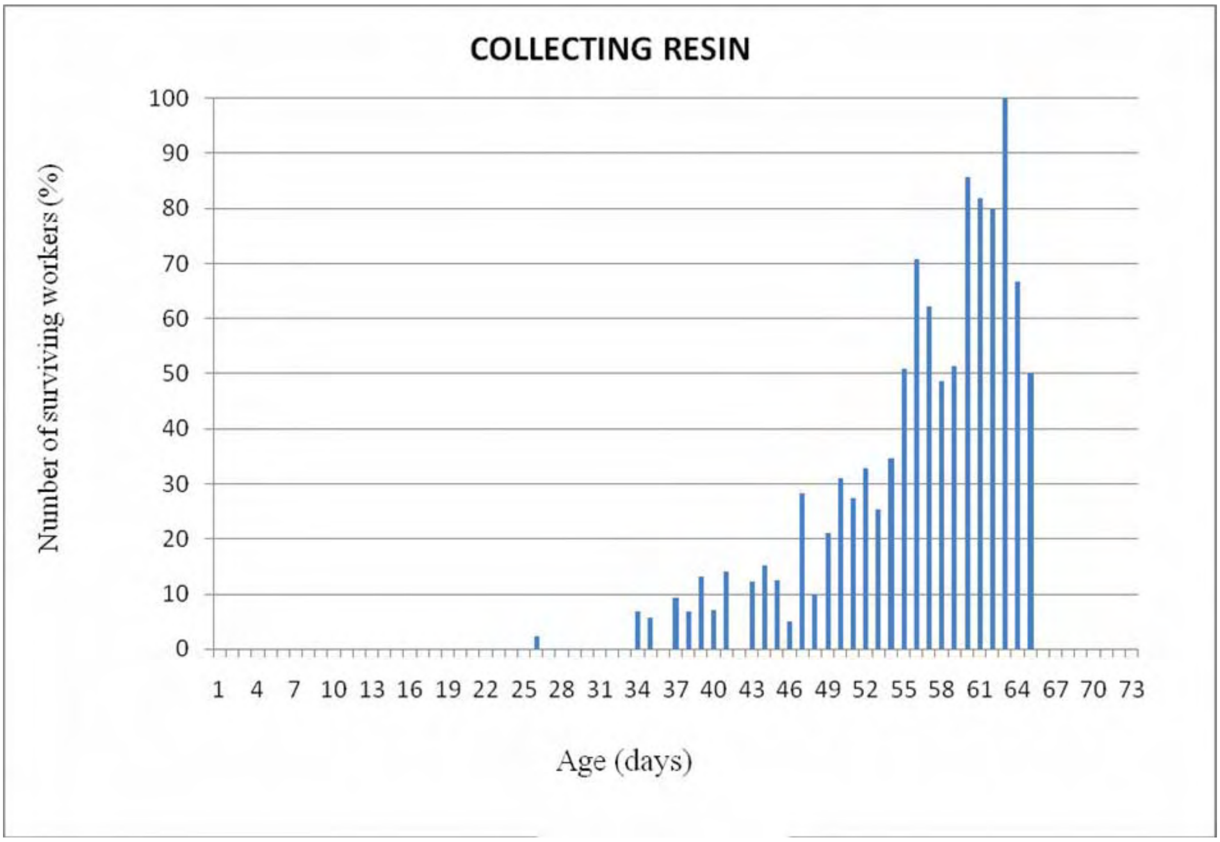


Figure 74. Frequency of workers of *M. becarri* engaged in collecting resin

Most workers collected resins during the mid and later part of their lifespan. Workers executing this task range in age from 25 to 65 days with the average period of activity at 17.3 days. The frequency of the workers ranged from 1-100%. The maximum frequency was attained with workers at 65 days old and workers between the ages of 52 and 66 days executed this activity with mush higher vigour with more than 50% participation. The average frequency of surviving workers involved in this activity was 34.4% (table 17).

5.4.2.6 Pollen collection

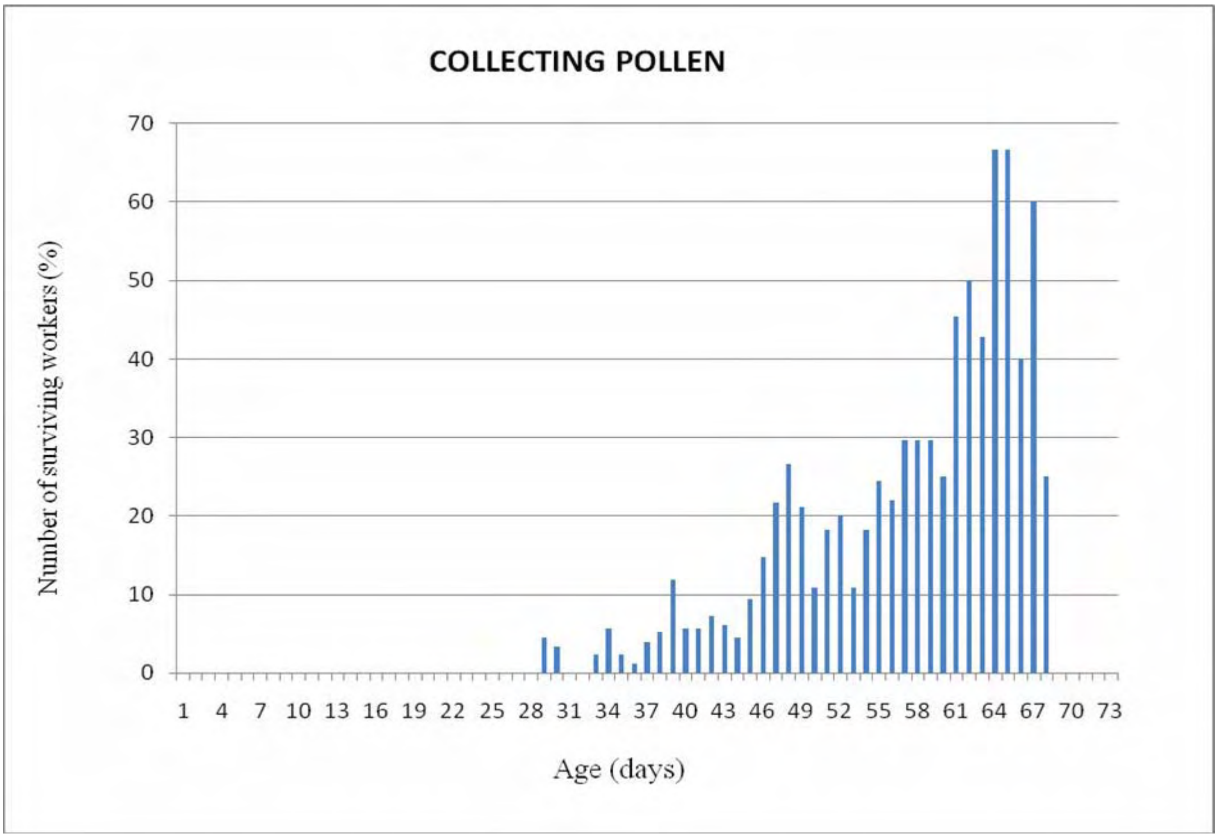


Figure 75. Frequency of workers of *M. becarri* involved in collecting pollen

Pollen collection just like resin collection is done mainly during the mid and later parts of the life span of the bees. Younger bees below the age of 28 days were never seen taking part in this task. On the average 21% of workers between the ages 28 and 68 days old collected pollen while most workers (>50%) were involved in collecting pollen at a later ages between 64 and 67 days. The maximum number of surviving workers (66.6%) performing this task was recorded at the age of 64 and 65 days. Predominantly, the activity, though being carried out by both middle age and older workers, workers older than 64 days are most likely to execute this activity unlike workers younger than 63 days.

5.4.2.7 Fanning nest

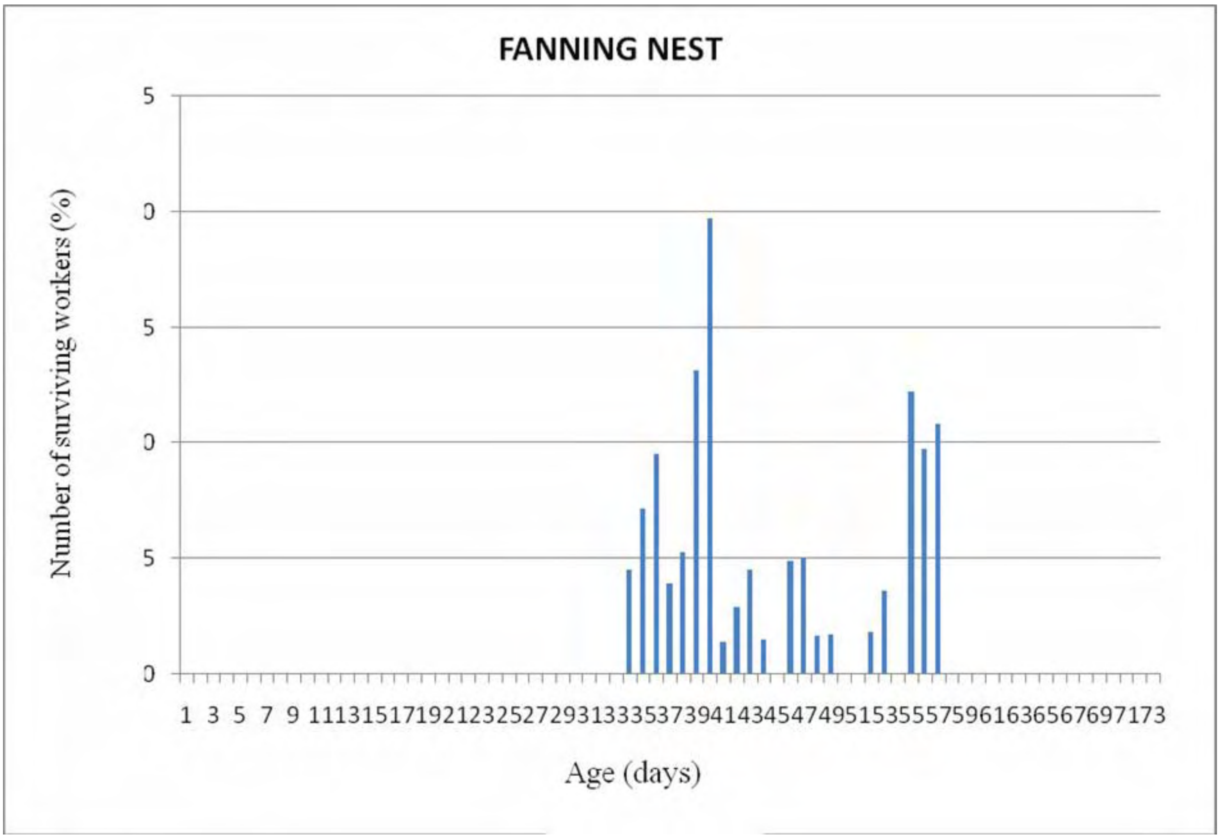


Figure 76. Frequency of workers engaged in fanning the nest inside the nest

This task mostly occurred between the 34th and the 58th days of the lifespan of the workers. Very few workers performed the task with the highest recorded surviving workers frequency at 20 % and the lowest at about 2 %. On the average about 6.2% of the workers would perform this task during their lifespan for an average period of 5.6 days (Table 17).

5.4.2.8 Guarding nest

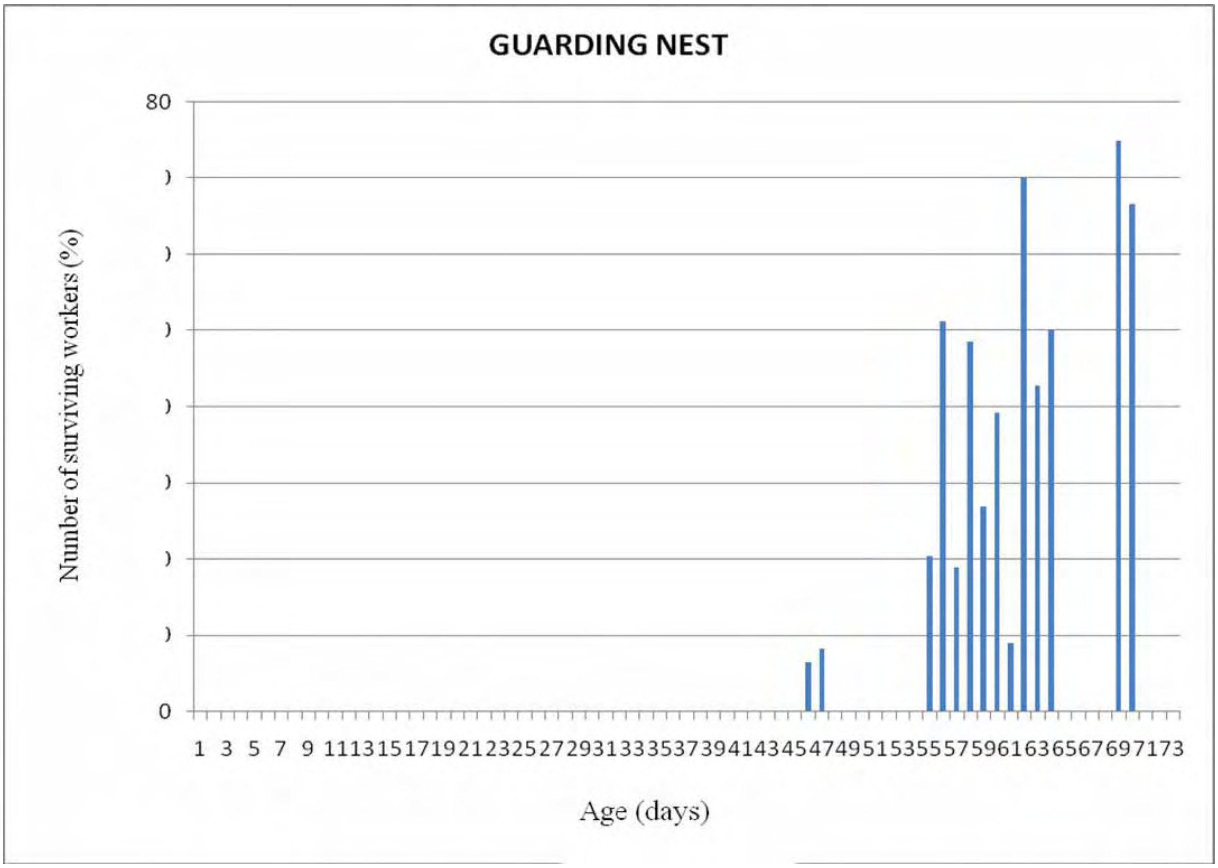


Figure 77. Frequency of workers of *M. becarri* engaged in guarding nest at the nest entrance.

The average period of workers guarding nest entrance was 7.6 days and the average frequency of surviving workers performing the activity was 38.1 % (Table 17). Most individual workers will guard the nest entrance during the last days of their lifespan between 55 and 70days. However, this activity is not restricted to just the older workers. Some younger and middle age workers also guarded the nest between the 46th and 47th days of their life span. More than 50% of the workers between the ages of 62 and 70 days are likely to perform this task in the colony.

5.4.2.9 Cleaning nest

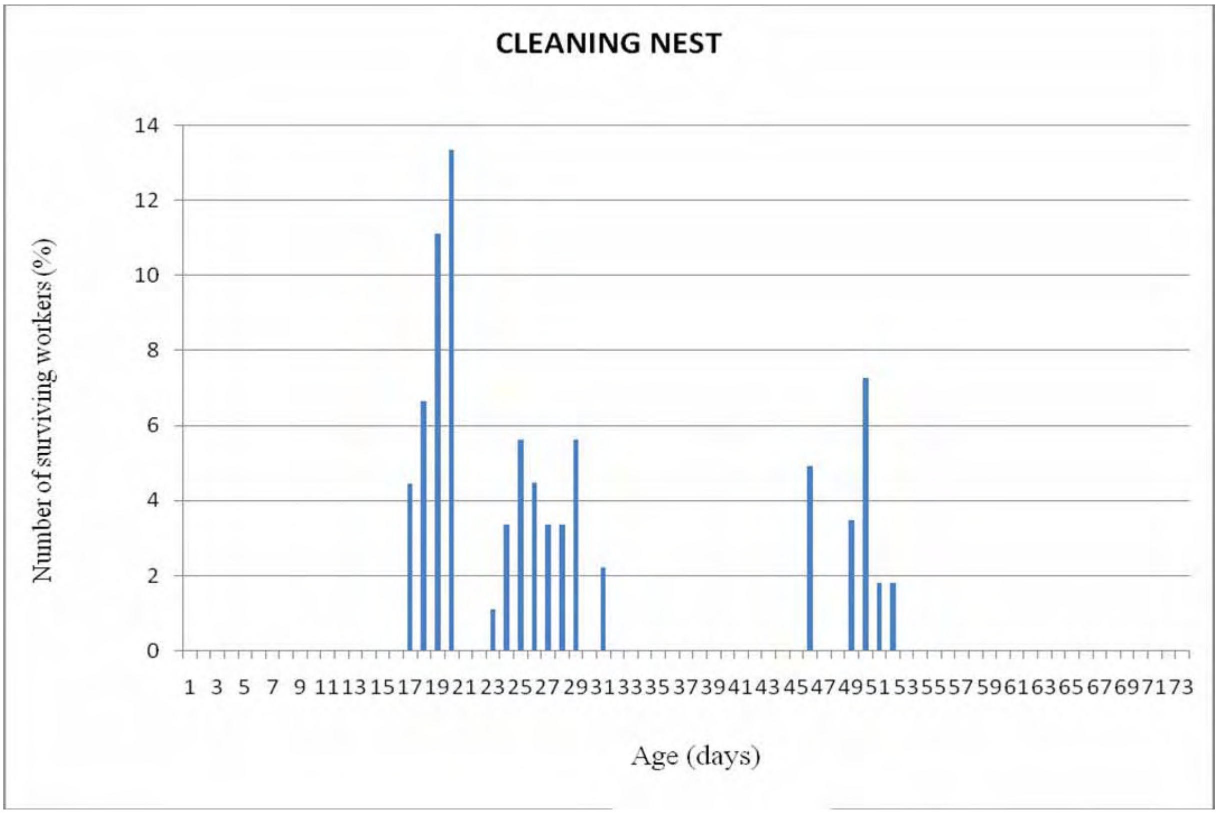


Figure 78. Frequency of workers of *M. becarri* engaged in cleaning the nest.

This is one activity that overlapped being performed by younger workers as well as older workers of *M. becarri*. Relatively fewer workers were involved in this activity. The maximum percentage of surviving workers engaged in this activity was 13.3%. The average duration of this task was 5 days meanwhile the average surviving workers that performed this activity was 4.94%.

5.5 Discussion

The duration of the lifespan of a workers of *Meliplebeia becarri* range between 24- 73 days with an average longevity of 52.7days (Figure 4). *Meliplebeia becarri* shows a much higher longevity compared to most species of stingless bees already studied in South America. Some examples are *Melipona compressipes fasciculate* with 42.5days (GIANNINI 1997): *Melipona bicolor*, 44.0 days (BEGO 1983): *Melipona favosa*, 40.0days (SOMMEIJER 1984) and *Scaptotrigona postica*, 39.5 days (SEMÕES & BEGO 1991).

Most workers of *M. becarri* survived the early days of their life cycle implying high mortality during foraging. According to JEANNE (1986), workers of *M. becarri* would exhibit polyethism. Workers of *M. becarri* seems to be specialize in only one set of tasks at given age groups though with some flexibility or overlap in some tasks like in cleaning nest, guarding nest entrance and pillar construction.

From the analysis of the activities of *M becarri*, the average frequencies of worker bees performing tasks were: Collection of resin (34.8%), construction of involucrum (33.3%), construction of pillar (31.1%) cerumen works (25.36%) and pollen collection (24.53%). However, up to 60% of the workers performed tasks related to foraging such as collection of resin and pollen. Compared to *Melipona compressipes fasciculate* shows a much higher frequency of foraging with 88.3% (GIANNINI 1997).

On the contrary the average duration of each activity is much higher for *M. ogouensis* than twice that of *M. compressipes* and that of *Scaptotrigona postica*.

The average days per activities were equally significantly high (Table 4.5.3) compared to that of *Melipona compressipes fasciculata* (GIANNINI 1997). Collection of resin (32.8 days), pollen collection (31.2 days), Cerumen (30.3 days), pillar construction (29.8 days) and involucrum (27.8days). *M. becarri* is a mongynous species with age polyethism.

5.6 Conclusion

Meliplebeia becarri are typical stingless bees with subterranean nests in the Bamenda highlands. The observed colonies were always with a single queen (monogynous condition). It is thus very likely that *Meliplebeia becarri* do not exhibit polygnnous conditions in their nests. However, stingless bee may have another queen when the colony wants to swarm or have another queen in prison waiting for a convenient time to be released. This happens when the existing queen is old enough. The second queen is kept in prison to ensure smooth continuity of the colony incase the older queen suddenly dies.

The workers of *M. becarri* are capable of living for as long as up to 73 days (approx. 11weeks) though averagely the life span of the workers is expected at about 52.7 days (approximately 8 weeks). The results from this research suggest that workers of *M. becarri*, perform tasks in the nests according to their ages.

6 General conclusion and recommendations

6.1 General conclusion

Stingless bees construct their nests in a wide range of habitats in the Bamenda highlands. The population of their colonies can ranged between 100 and 6000 individuals depending on the species and age of colony. The designs of nests architectures in stingless bees differ from species to species. Brood cells and storage pots are organized differently.

Behavioral studies show that queen-worker interactions can be simple or ritualized accordingly. The queen behavior at any time, will depends on the level at which the cell construction process is progressing. Queen is more active and agitated when cells are already at the collard heights.

The workers of stingless bees do perform tasks related to grooming of nest, nest reconstruction, hygiene, ventilating nest and foraging at different stages of their life span.

Forager seems to be willing to go for any distance in search of quality food. However, the willingness for foragers to forage far away from their nests will depend on a number of factors: availability of food in store, quality of food and availability of other alternatives food sources nearby the nest.

6.2. Recommendations

1. Substantial studies on all aspects of wild bees and stingless bees should be highly encouraged given the importance of bees in pollination and honey production.
2. There is need to breed bee taxonomists and ecologists to be able to conserve and monitor bee diversity and other pollination services in Cameroon.
3. Rural communities who are always in contact with these bees deserves to understand the importance and benefits of stingless, thus there is an urgent need for awareness campaigns to educate communities on these bees.
4. Protection of native bees and their population is urgently needed in order to guarantee their future.
5. Meliponiculture should be developed urgently in the region to avoid further destruction of colonies which can possibly lead to species erosion.

7 Summary

The Bamenda highlands of Cameroon were once largely covered with montane forests. However, with persistent pressure on these forests for farming and grazing purposes, only patches of the montane forests remain today. The remaining afro-montane forest patches are unique sites with high level of endemism of both plants and animal species. These forests patches are recognized globally as important sites for conservation of biodiversity. Most studies done so far in this area focused on large mammals, birds and plants. Until now almost nothing is known about invertebrates such as wild bees in this area. The aim of this study was to bring out the diversity of stingless bees in this area with main focus on the nest biology and behaviour of species.

Firstly, the site was assessed to determine the number of species of stingless bees present in the area. Six species of stingless bees grouped into four genera exist in the Bamenda afro-montane forests. The four genera are: *Meliponula* (3 species), *Dactylurina* (1species), *Hypotrigona* (1 species) and *Liotrigona* (1species). The most represented of the species in Bamenda was *Liotrigona*.

The habitat preferences and nest architectures of the six species was studied. More than 25 nests were excavated and detail measurements of the different nest structures were taken. Stingless bees in the Bamenda highlands were found to have huge variations in habitat preferences. Both subterranean and exposed nests were studied. Nest designs differ with species as well as the habitats of the species. Nest were found in tree trunks, mud walls, traditional hives, in soils or even just attached to tree branches. Brood cells and storage pots differ from species to species. Some species constructs combs while others construct cluster cells.

This study went further to investigate the behavior and the process of food provisioning and oviposition in *Hypotrigona gribodoi*. More than 30 video recordings and focused observations were made under artificial hive condition. Generally, the queen stays most of her life on the brood cells. Cells are constructed in clusters and without any particular plane at the surface to distinguish the newly constructed cells from the old. These bees exhibit semisynchronous brood cell construction with exclusively batched queen oviposition. Workers of *H. gribodoi* clean their nest during the early hours of the day and dump the dirt just below the nest entrance. Workers

were never seen laying trophic eggs. *Hypotrigona gribodoi* are generally calm during manipulation. No case of attack on body parts was registered during the research period. The queen can only become aggressive when deprived of her privilege to lay an egg into already provisioned cells. Though just one queen was found in the colony throughout the study period, it is possible to have a second queen in some species.

Meliplebeia becarri was used to study the pattern of tasks partitioning among workers of stingless bees. 90 workers were marked and 9 activities followed throughout the life span. Results showed that the lifespan of a workers of *M. becarri* range between 24- 73 days with an average longevity of 52.7days. Workers of *M. becarri* specialize in only one set of tasks at given age groups though with little overlap in some tasks like in cleaning nest, guarding nest entrance and pillar construction. Activities related to reconstruction of the nest were done by workers between the ages of 02 - 29 days meanwhile foraging was mostly done by workers between 25 - 68days old. Guarding of nest was mainly by workers above 55days old. Cleaning of nest was done both by workers of ages between 17-29 and 49-53days

Different species of stingless bees behave differently in their tasks allocations and in interactions between the queen and workers. Thus, more specific studies on stingless are recommended to for further understanding of aspects of diversity of these bees in Cameroon.

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Appendix 1. **List of Tables**

Appendix 2. **List of Figures**

Appendix 3. Coordinates of areas where bees were collected

Location	**Coordinates**
Ako	689107, 755421
Mbasang	702729, 712175
Ndu	697968, 710059
Dom	676014, 706356
Chaw	671253, 701859
Takija	689900, 697231
Njottin	673105, 695908
Simonkoh	668740, 690618
Elak	665698, 689692
Abuh	651548, 698173
Belo	649564, 682022
Babanki	642687, 675806
Ndop	656573, 662184
Lip	712383, 666284
Maboua	711722, 661391

Appendix 4. Pattern of dead of marked worker bees of *Meliplebei ogouensis*
(Numbers in the column of batches denotes life span of each bee in days)

	Days of disappearance					
Marked workers	Batch 1	Batch 2	Batch3	Batch4	Batch 5	Batch6
1	35	43	24	35	35	56
2	35	45	33	37	37	56
3	37	45	37	37	37	56
4	40	46	37	40	40	57
5	40	47	37	40	43	57
6	43	50	42	46	46	57
7	49	50	42	49	49	57
8	55	55	55	55	55	60
9	60	56	55	60	60	60
10	60	56	61	61	61	60
11	62	56	62	62	62	60
12	62	56	62	62	62	61
13	62	56	62	62	62	61
14	62	60	63	63	63	61
15	68	73	64	70	71	66

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