Pot-Honey

A Legacy of Stingless Bees

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3. Australian Stingless bees

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Abstract (additional to published chapter)

To date, there has been relatively little formal research conducted on Australian stingless bees.

However, the wealth of knowledge held by stingless bee enthusiasts is invaluable. Further

scientific studies are needed to support these beekeepers and to help improve techniques in

colony propagation, queen rearing, drone rearing and, possibly, artificial insemination. The

reported successful pollination services provided by stingless bees overseas have yet to be

realised in Australia. It is hoped that further research will continue to enable us to uncover more

of the mysteries of our unique bees, and to develop their potential.

Keywords: *Austroplebeia* • *Trigona* • Indigenous Australians • Australian stingless bee

industry • pests • pollination • fighting swarm

Introduction

Stingless bees have been an important part of indigenous Australian culture for millenia

however, modern meliponiculture in Australia is still very much in its infancy (Heard and Dollin,

2000). A recent survey showed that interest in stingless bees is growing and Australians are

becoming

increasingly aware of and concerned about conservation of these species. More community members are keeping hives with this interest in mind (Halcroft, unpublished data). Beekeepers in the northern regions are able to produce honey in small quantities and some multiply hives for profit.

Of the two stingless bee genera in Australia, *Trigona* (*s.l.*) is the most studied. The domestication of *Trigona carbonaria* colonies began in the 1980s and Dr. Tim Heard conducted ground-breaking work in *T. carbonaria* husbandry (Heard, 1988b, a). As a result, most scientific research has been conducted on this species. Few studies have been conducted on *Trigona* (*s.l.*) pollination efficacy, and have mainly used *T. carbonaria* or *T. hockingsi* in macadamia nut (*Macadamia integrifolia*) crops. Pollination studies on other horticultural crops are minimal and, as such, anecdotal reports pertaining to crop pollination are cited here.

Austroplebeia have only recently become of interest to beekeepers and hobbyists. A small number of studies have been conducted on aspects of biology of *A. australis* and *A. symei*, as their brood structure and queen /worker interaction is more easily observed than that of *Trigona* (*s.l.*), due to reduced nest structures. Recent doctoral research has been conducted (M. Halcroft) to better understand the development of the Australian stingless bee industry, phylogeny of *Austroplebeia*, the biology and behavior of *A. australis,* and to assess the ability of *A. australis* to pollinate crops in greenhouse and field settings. This research is incomplete and ongoing, and therefore, is cited here as unpublished data.

Although Australian stingless bees are not as diverse in size or morphology as Neotropical or Paleotropical species, our bees are proving to be diverse and resilient in their behavior. Their native range is mostly limited to the northern half of the continent; however, *T. carbonaria* has a distribution that reaches the southernmost range of any stingless bee species (Dollin et al., 1997). *Austroplebeia* occur in some of the most arid areas of Australia, where the climate extremes are harsh and the food resources are often scarce. Australian stingless bees have evolved diverse behaviors to survive under such conditions.

While few scientific studies have been conducted on the behavior of Australian stingless bees, amateur beekeepers often have a wealth of knowledge and their experience is extremely valuable. Communication with experienced beekeepers is of utmost importance when initiating research, and anecdotal accounts are appropriately cited here. While there is great potential for further research on stingless bees in Australia, this chapter aims to provide an overview of current knowledge and suggest areas for further study.

3.1 Indigenous Australians and their relationship with stingless bees

Indigenous Australians have been collecting the strong, tangy honey from stingless bee nests 1sugarbag' for centuries. Hockings (1883) first reports the Australian *Trigona* (*s.l.*) and *Austroplebeia* from his visit to northern regions of Queensland, where local Aboriginal people call these bees "karbi" and "kootchar", respectively. It is unclear which tribal language Hockings refers to in his paper.

There are many different Australian Aboriginal tribes. The Aurukun on Cape York, in far north Queensland, is the homeland for the Wik Mungkan people. In 2003, an industry based on stingless bees and traditional culture was the inspiration for a group of 50 Wik school children, aged between 12 and 16 years. Using the natural resources of their homeland, the sugarbag "may man-pathan" provided the prospect of making real money and building a culturally-based business. The children within this indigenous community developed a business plan, and become more motivated and engaged in learning (Yunkaporta, 2009). Anecdotal accounts of indigenous bee hunting methods are described in bush tales, and these include: placing a fine hair or grass into the terminal abdominal segment of a forager, which is used as a flag to follow it back to the nest; sprinkling foragers with flour to make them easier to see and follow; and bee hunters relying on the loud humming sound of a predatory wasp (*Bembix*) which hovers outside the nest entrance, waiting for foragers to leave (A. Beil, personal communication).

Figure 3.1 Indigenous Australian axes. Photo G. Walsh - www.hogartharts.com.au

Traditionally, honey "may at" or "may kuyan" is used for medicinal and culinary purposes, while the cerumen "wom" is used as a waterproofing agent for baskets, as a wood preservative, as glue to secure axe heads "thayan" (Figure 3.1) and for personal and artefact decoration (Rayment, 1935; Yunkaporta, 2009; Welch, 2010). Cerumen has also been found in protective covers, fashioned around ancient rock paintings, to protect them from rain and erosion (Rayment, 1935). Pellets of cerumen are used in some rock art, notably in the Kimberley Ranges in Western Australia, to create shapes of humans, dingoes, turtles and spirit figures on the rock surface (Welch, 1995). This collage technique (Brandl, 1968) permitted incorporation of organic materials in a normally inert, inorganic rock face. Beeswax and plant resins are extremely amenable to carbon dating because storage of fresh products within hives, and consequent use by indigenous craftsmen, , enable accurate estimates of when the collages were created, thus dating the artwork (Bednarik, 2002). Interest in indigenous culture and art has increased over the past 20 years and is at a peak in popularity (Artlandish, 2010). Cerumen is still used by Australian Aboriginal artists and craftsmen to manufacture hunting tools such as spears "kek" and

woomeras "thul", as well as firesticks "thum pup" and mouth pieces for didgeridoos, a traditional musical instrument (Yunkaporta, 2009).

Sugarbag honey can fetch very high prices in comparison to honeybee honey. In 2005, Russell and Janine Zabel commenced a training programme in sugarbag harvest and colony transfer within the Aurukun, with the aim to develop a sustainable industry based on sale of sugarbag honey and cerumen (Zabel, 2008). An Australian government grant was received to assist development of this new enterprise, which had potential to boost local employment and would be consistent with the rapidly-developing ecotourism industry.

In 2010, an industry based on sugarbag is seen as an option for inclusion in a preliminary proposal for the Department of Aboriginal Business Development, in Grafton, in northern New South Wales. This proposal is investigating indigenous land development in the Northern Rivers region using traditional cultures and sustainable practices (Lain, 2010). Another initiative is the Thamarrurr Development Corporation proposal to develop a wildlife industry in Wadeye, Northern Territory, including health products containing sugarbag honey (Adlam, 2010). Potentially, stingless bees could provide sustainable income for both Australian indigenous and non-indigenous communities through production of honey, cerumen, bee colonies, and pollination service.

3.2 Australian stingless bees

There is much needed change regarding classification of the genus / subgenus group name of *Trigona* (*Heterotrigona*), which includes a portion of the native Australian Meliponini. At present, according to Michener (1990, 2007) species of *Trigona* (*s.l.*) that occur in the Indoaustralian regions are of the subgenus *Heterotrigona*. Recent molecular studies, and also morphology, suggest this taxonomic classification is incorrect and that Australian species previously named *Trigona* (subgenus *Heterotrigona*) should be changed to the genus *Tetragonula* Moure, 1961 (Rasmussen and Cameron, 2007; Rasmussen and Cameron, 2010).

There are many species and subgenera to consider in Asia and Australia, with 15 species in Australian comprising two genera. We have chosen to preserve the group name *Trigona* (*Heterotrigona*) in this chapter, until further taxonomic and systematic research is decisive. The bees in Australia are small (< 4.5 mm) and black. However, *Austroplebeia* can be distinguished from *Trigona* (*s.l.*) by coloured body markings, thoracic shape and nest architecture.

The highest rainfall areas within Australia occur in the northern, eastern and far south eastern coasts (BOM, 2010a) (Figure 3.2), resulting in tropical, subtropical and temperate forest and woodland vegetation. The natural range for Australian stingless bees is in the tropical and subtropical regions of northern Australia, with the exception of *T. carbonaria*, which has, by far, the southernmost distribution. The temperature threshold for flight activity in *T. carbonaria* (Heard and Hendrikz, 1993) is > 18°C, and for *A. australis* > 20°C (Halcroft, unpublished data), which means foraging periods are substantially reduced for colonies in the most southerly range of their distribution.
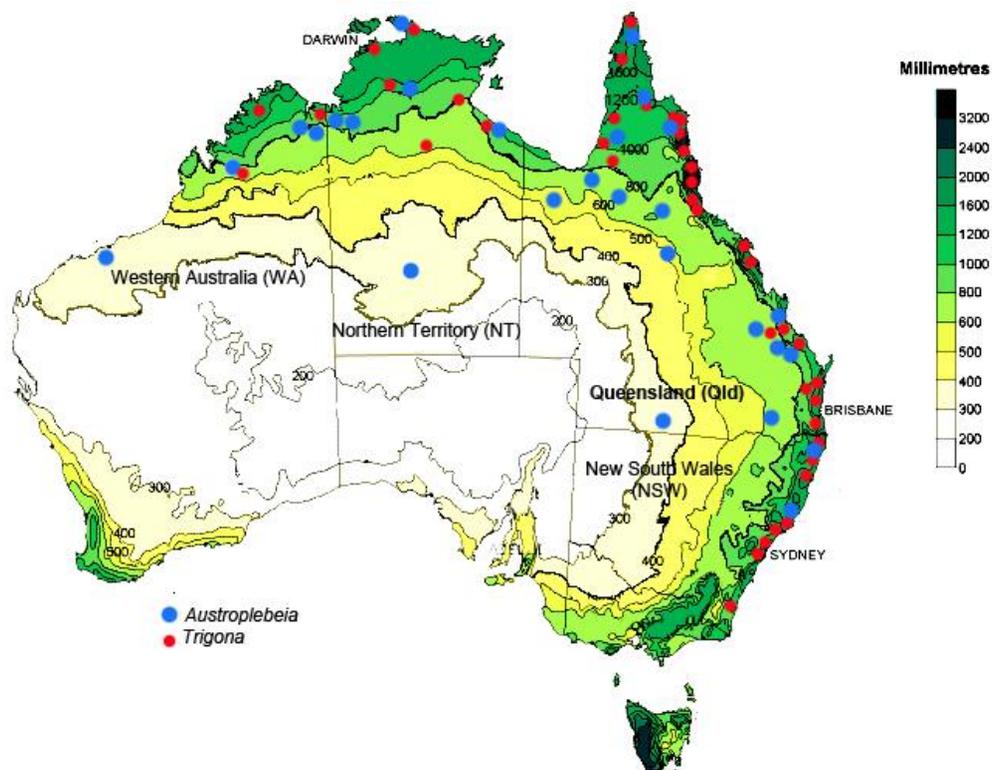

Figure 3.2 Reported distribution of Australian stingless bees. (Dollin et al. 1997; Dollin 2010 unpublished data)

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3.2.1 Castes and genders of the Australian stingless bees

As with all stingless bees species there are two castes—queen and worker. All Australian species are thought to be monogynous. However, the incidence of virgin queen imprisonment in queenright colonies of *A. australis* has been observed (MH, personal observation) (Figure 3.3). Queens can be identified by their long, pale abdomen and short wings (Figure 3.4). They are usually found on the brood, although extensive nest patrolling is not uncommon in *A. australis* (MH, personal observations).

Figure 3.3 Imprisoned *Austroplebeia australis* virgin queen. Photo M. Halcroft.

Figure 3.4. *Austroplebeia australis* queen with workers on brood. Photo M. Halcroft

Trigona (*s.l.*) drones are difficult to identify within the hive, without the aid of a magnifying glass, as they have no defining markings (Dollin, 2010a). Their bodies are slightly more slender and the antennae are longer, having one additional segment, compared to females or workers (Michener, 2007). They frequently form drone swarms outside nests and sometimes aggregate on foliage at night. These aggregations and swarms can be seen for a number of days when conditions are favourable (Klumpp, 2007). *Austroplebeia* drones are easier to identify within the nest because the cream-colored markings on their thorax are more pronounced, and they also have markings on the abdomen and legs (Dollin, 2010a) (Figure 3.5). Their apparently slimmer bodies and constant movement of the antennae, as they move, also distinguishes them (MH, personal observation). *A. australis* drones also form mating swarms and aggregations, although these are not as large as those of *Trigona* (*s.l.*) (MH, personal observation). *A. australis Au. australis* colonies appear to produce drones in 'batches' or 'male-producing periods' (MPP) (Velthuis et al. 2005), with drones being present only periodically in a single colony. It is not clear whether drone production is curtailed during periods of resource scarcity.

Figure 3.5 *Austroplebeia australis* drone showing cream markings on legs and thorax. Photo M. Halcroft

3.2.2 Brood production

In the Meliponini, brood production is an elaborate procedure and involves a sequence of interactions between the queen and a group of workers (Sakagami et al., 1973; Sakagami 1982). This temporal sequence is termed the 'provisioning and ovipositing process' or "POP" (Sakagami SF and Zucchi R, 1963; Michener, 1974; Wittmann et al., 1991). Cells are mass-provisioned with a mixture of honey, pollen and protein-rich secretions from the hypopharyngeal glands (Michener, 1974; Silva de Moraes et al., 1996). Some species provision cells successively while others provision synchronously (Sommeijer and Bruijn, 1984). Once a cell is provisioned, the queen oviposits and workers seal the cell (operculation) (Drumond et al., 1999). *Trigona carbonaria* constructs and provisions brood cells synchronously, and the queen oviposits in batches (Yamane et al., 1995). *Austroplebeia australis* and *A. symei* construct and provision brood cells in a successive pattern, while the queen does not oviposit in batches (Drumond et al., 1999).

Meliponine queens normally mate only once (Kerr et al., 1962; Michener, 1974), returning to the nest with the male genitalia still caught in the vagina (Michener, 1974). The incidence of low frequency polyandry has been reported in *Melipona beecheii* and *Scaptotrigona postica,* (Paxton et al., 1999); however, it is thought that most stingless bees are monandrous, including the Australian species (Drumond et al., 2000; Green and Oldroyd, 2002). Sperm is stored in her spermatheca. A diploid female is produced when a sperm cell is released to fertilise the egg as it passes through the oviduct. If sperm is not released, the egg is not fertilised and a haploid male is produced (Michener, 2000). While drones are normally produced by the queen, laying workers have been reported in some Brazilian species of *Melipona* (Koedam et al., 2005; Koedam et al., 2007). Although this is rare in Australian stingless bees (Michener, 1974; Drumond et al., 1999; Tóth et al., 2004), *A. australis* and *A. symei* workers have been observed laying small numbers of trophic eggs in queenright colonies. On all recorded occasions the queen consumed those eggs

(Drumond et al., 1999). Microsatellite analysis determined that workers were not responsible for drone production in queenright colonies of *A. australis, A. symei* or *T. carbonaria* (Drumond et al., 2000; Gloag et al., 2007). Drone production has been observed in some queenless colonies (Klumpp, 2007; MH, personal observation); however, this has not been studied in sufficient detail.

3.3 Characteristics of Australian stingless bees

3.3.1 *Austroplebeia*

Nine species of *Austroplebeia* are listed in the Zoological Catalogue of Australia (Cardale, 1993), and the most commonly domesticated and studied species are *A. australis* and *A. symei*. Species descriptions for this genus are inadequate for effective identification and no working key exists at present. Ongoing research in the areas of molecular, morphological and morphometric analysis suggests that there are only 3 to 6 species of *Austroplebeia* in Australia (Halcroft and Dollin, unpublished data). Only one of these, *A. cincta*, occurs outside Australia, in Papua New Guinea (PNG) (Moure, 1961; Rasmussen, 2008).

Current classification is based mainly on variations in body markings. Mature adult bees are black, with varying levels of cream / yellow markings on the scutellum of their thorax and on their face (Michener, 2000). Bees measure between 3.5 and 4.5 mm, and species characteristics are presented in Table 3.1 (Michener, 1961; Dollin, 2010a).

Table 3.1 Explanation of color markings used to classify species in the genus *Austroplebeia* (Cardale 1993; Dollin 2010). Dark markings represent cream / yellow markings on black bees.

Species name	Native range	Description	Markings
Austroplebeia symei Rayment 1932	Qld & NT	4.5 mm, darkest with little or no markings on the face and thorax	
A. australis Friese 1898 *A. cassiae* Cockerell 1910	Qld & NSW	4 mm, four distinct cream markings on the scutellum. Minimal facial markings.	
A. cockerelli Rayment 1930	NT	3.5-4 mm. Facial markings more extensive but vary in degree. Broad cream markings on thorax, mesothorax narrow stripes each side.	
A. essingtoni Cockerell 1905	NT		
A. ornata Rayment 1932	Cape York, Qld		
A. percincta Cockerell 1929)	Central NT		
A. websteri Rayment 1932	WA		
A. cincta Mocsary 1898	PNG & possibly Qld	3.5 mm. Distinct facial and thoracic markings.	

3.3.1.1 Natural distribution

Dollin (2010b) found that *Austroplebeia* occurs throughout northern Australia (Figure 3.2).

A. australis and *A. symei* have the widest distribution. Specimens currently considered to be

A. symei have been collected along the east coast from Cape York (11°04'S) to Kilcoy in

Queensland (26°57'S), as well as the northern areas of the Northern Territory. *Austroplebeia*

australis is found coastally, as far south as Kempsey, New South Wales (31.08ºS, 152.82ºE,

elevation 10 m) and inland near Inverell, New South Wales (29.46°S, 151.06°E, elevation 584

m) and also occurs in arid regions of inland Queensland. The remaining species are found mainly in northern Queensland, Northern Territory and Western Australia, with *A. percincta* originally described from an arid region of central Australia (Cockerell, 1929).

While *Trigona* (*s.l.*) is commonly found in areas of high rainfall, many *Austroplebeia* thrive in areas that experience low annual rainfall (300 – 600mm) and extreme temperature ranges (-3 – 40.5°C) (A. Dollin, personal communication, 2009; BOM, 2009). Until recently, it was thought that *Austroplebeia* were more sensitive to low temperatures, resulting in their northerly restricted distribution. Current research has revealed that colonies of *A. australis* are able to survive subzero temperatures, without actively thermoregulating the nest. These colonies were shown to contain developing brood throughout the year (Halcroft, unpublished data).

3.3.1.2 Nest architecture, colony population and brood structure

Similar to *Trigona* (*s.l.*), *Austroplebeia* chooses tree hollows, but cavity diameter is usually smaller. *A. australis* is found in cavities 50 – 110mm in diameter (Halcroft, unpublished data). A smaller species found near Normanton, Queensland, may occupy cavities in coolabah (*Eucalyptus coolabah*, Myrtaceae) trees with a diameter of only 35 mm (A. Beil, personal communication, 2009). Some colonies of *A. australis* have been found in narrow tree limb hollows up to 6 m in length (R. Zabel, personal communication, 2008). A recent nest survey conducted in south-east Queensland showed that dead trees comprised over 87% of nest cavities chosen by *Austroplebeia* in that area (Halcroft, unpublished data).

Estimates of colony populations in *Austroplebeia* have not been studied in detail; however, recent studies have shown that, within natural nests, brood populations can range from 2,000 to 13,000, averaging of 5,000 (Halcroft, unpublished data). All *Austroplebeia* construct spherical brood cells and, with the exception of *A. cincta* (see Table 3.1), make simple cell clusters (Michener, 1961; Dollin, 2010a) (Figure 3.6a). Open cells face outwards from the leading edge

of the cluster, in irregular directions. Clustered brood cells can be constructed to fit into the narrow, irregular cavities of the smaller trees or large limbs favored by *Austroplebeia.*

The New Guinea species, *A. cincta,* is the only *Austroplebeia* found outside Australia (Moure, 1961). Recently, however, some colonies resembling *A. cincta* have been found in Queensland (Dollin, 2010a). Nests of these newly discovered colonies have not been examined, and studies are in progress. Unfortunately, no photographs of *A. cincta* nests or brood structures are currently available.

*Addendum: see Dollin (2013) *Austroplebeia cincta*: A spectacular new species of stingless bee for Australia. *Aussie Bee Online*, Article 22, January 2013. Available at www.aussiebee.com.au/aussiebeeonline022.pdf

3.3.2 *Trigona* (*s.l.*)

Identification of Australian *Trigona* (*s.l.*) is very difficult in the field. Some species, especially *T. carbonaria*, can vary considerably in size according to geographic location (Dollin et al., 1997). The largest bee is *T. hockingsi*, measuring approx. 4.5mm in length, while the smallest is *T. clypearis*, 3.5mm in length (Klumpp, 2007). Species within the *carbonaria* species-group are difficult to separate on their body size or morphology. Thus, nest architecture is an invaluable tool in the accurate identification of species (see Nest architecture).

The currently described Australian *Trigona* (*s.l.*) are classified into three species-groups (Dollin et al., 1997; J. Klumpp, personal communication, 2010; A. Dollin, personal communication, 2010), namely:

Iridipennis group Sakagami 1978

   T. (*Heterotrigona*) *clypearis* Friese, 1908

Laeviceps group Sakagami 1978

   T. (*H.*) *sapiens* Cockerell 1911

Carbonaria group Dollin et al. 1997

T. (*H.*) *carbonaria* Smith 1854

T. (*H.*) *hockingsi* Cockerell 1929

T. (*H.*) *mellipes* Friese 1898

T. (*H.*) *davenporti* Franck 2004

3.3.2.1 Natural distribution of *Trigona* (*s.l.*) in Australia

Dollin et al. (1997) report that *T. clypearis* and *T. sapiens* are restricted to the Cape York

Peninsula in northern Queensland (18°0'S – 10°56'S) compared to the *carbonaria* species-

group, distributed throughout northern and eastern Australia. The most recently described

Trigona (*s.l.*), *T. davenporti*, was discovered by Peter Davenport, a local beekeeper who helped

to pioneer stingless beekeeping in Australia (Klumpp, 2007; Dollin, 2010c). So far, this species

has only been reported within a restricted area around the Gold Coast in south eastern

Queensland (A. Dollin, personal communication, 2008). *T. carbonaria* is the most widely

distributed species*,* occurring along much of the east coast of Australia. It is found as far north as

the Atherton Tablelands in Queensland (17°15'S) and as far south as Bega, in New South Wales

(36°40'S) (Figure 3.2). *Trigona carbonaria* chooses large tree cavities that may provide superior

insulation against the weather extremes experienced in its most southerly locale. Tse

(unpublished data) found that both *T. carbonaria* and *T. hockingsi* maintain the brood chamber at

significantly higher temperatures than the nest cavity or ambient temperature. These studies were

not, however, conducted during periods of temperature extremes and further studies would be

beneficial to better understand temperature regulation, especially by *T. carbonaria.*

3.3.2.2 Nest architecture, colony population and brood structure

Tree cavities are the most commonly chosen nest substrate for *Trigona* (*s.l.*) in Australia. They

can also be found inside water meter boxes, stone walls, beneath concrete foot paths and within

door and wall cavities. Nest entrance modifications vary, depending on species; however, environmental factors such as weather and predators can also influence those structures (Dollin et al., 1997). *Trigona carbonaria* often daub the area around the entrance with significant amounts of resin, whereas *T. hockingsi* and *T. davenporti* generally leave their entrances unadorned (Dollin, 2010a). *Trigona mellipes, T. sapiens* and *T. clypearis* build entrance tubes of varying sizes (Table 3.2), although they do not always do so.

Table 3.2 Comparative description of nest entrance characteristics within *Trigona* and *Austroplebeia* species. *Trigona* species (Dollin et al. 1997; Klumpp 2007), *Austroplebeia* species (unpublished data, Halcroft & Dollin 2010) and *A. cincta* (Michener 1961).

Species	Average entrance tube length (mm)	Average nest cavity diameter (mm)	Brood structure
T. hockingsi	None seldom smear entrance with resin	145	Horizontal steps/terraces. Hexagonal comb.
T. carbonaria	None smear entrance with resin +++	198	Flat spiral, single layer. Hexagonal comb.
T. mellipes	16	82	Similar to *T. hockingsi* but smaller.
T. sapiens	6	58	Irregular, horizontal or diagonal layers. No hexagonal comb.
T. clypearis	28	78	Roughly arranged in diagonal rows. No hexagonal comb.
A. australis	none to ~20mm	52-110	Clustered
A. ornata or *cockerelli*	none to ~20mm	35	Clustered
A. cincta (PNG)	20-80	45	Irregular concentric layers of one cell thickness, with bee space between layers

It has been estimated that a strong colony of *T. carbonaria* has a population of approximately 11,000 workers (Hoffmann, unpublished data). Brood volume can vary 940 – 3,535 ml in *T. carbonaria* and 1,100 – 2,550 ml in *T. hockingsi* (Dollin et al., 1997); however, *T. hockingsi* is able to build much larger nests if provided with the appropriate nest cavity (A. Dollin, personal communication, 2010). Both *T. davenporti* and *T. hockingsi* build brood areas with similar structure; however, *T. davenporti* has a smaller adult population. *T. mellipes, T. sapiens* and *T. clypearis* have much smaller nests and average brood volumes measure 595 ml, 224 ml and 464 ml, respectively (Dollin et al., 1997).

All Australian *Trigona* (*s.l.*) build elongated, vertically-oriented brood cells in regular, or nearly regular, structures (Dollin et al., 1997). There are, however, distinguishing features within these structures that can aid in species identification. *Trigona carbonaria* (Figure 3.6b) builds single layers of comb, arranged in a horizontal spiral. Brood cells are constructed on the outer rim of up to three circular spirals, at a time. The spiral formation can be clockwise or counter-clockwise. Brood construction can become erratic if the nest is disturbed, e.g. if the tree is felled (A. Dollin, personal communication, 2010). *Trigona hockingsi* (Figure 3.6c) builds a regular, horizontal brood structure with hexagonal comb, which is best described as terraced or stepped; it is not in a single layer. Both *T. davenporti* and *T. mellipes* build brood comb similar to that of *T. hockingsi*; however, the brood comb area of *T. mellipes* is considerably smaller (J. Klumpp, personal communication). Neither *T. sapiens* nor *T. clypearis* (Figure 3.6d) have a hexagonal comb structure because individual cells are arranged irregularly, in horizontal or diagonal layers.

Figure 3.6 Australian stingless bee brood structures. (a) *Austroplebeia australis* **(b) Trigona** *carbonaria*, **(c)** *Trigona hockingsi* , **(d)** *Trigona clypearis.* **Photos: (a – b) M. Halcroft, (c – d) R. Brito**

3.4 Behaviour of Australian stingless bees

3.4.1 Guard and forager behavior

Australian *Trigona* (*s.l.*) colonies usually employ at least 4 – 5 guards at the entrance (Yamane et al., 1995; MH, personal observation), with higher numbers occurring around the front of the nest on warm days (Klumpp, 2007). Guards are not normally aggressive towards human onlookers; however, if the nest is opened workers can become moderately to strongly aggressive (Michener, 1961). *Austroplebeia* guards occur in small numbers within the entrance of the nest but they withdraw into the entrance tube if observed too closely. When colonies are opened, workers are not aggressive (Michener, 1961), they buzz around the heads of human 'predators' and daub their hair with globules of resin until the nest is sealed (MH, personal observation).

Australian *Trigona* (*s.l.*) have evolved mostly in high rainfall areas (Figure 3.2), which provide consistent, reliable floral resources. *Austroplebeia,* on the other hand, have evolved mainly in arid regions, with evidently unreliable resources (Figure 3.2). Based on detailed observations, *T. carbonaria* and *T. hockingsi* workers appear to be 'curious and flighty', whereas *A. australis* and *A. symei* are 'shy and cryptic'. In 2009 (Halcroft, unpublished data) a parallel study was conducted to compare foraging behaviour and energy efficiency of three Australian stingless bees; *T. carbonaria, A. australis* and *A. symei*. The following information is based on this study. When provided with the same floral resources,*T. carbonaria* sent out nine times as many foragers as *A. australis* and four times as many as *A. symei*. Even when the floral resources were completely depleted, *T. carbonaria* continued to send foragers from the nest, while *Austroplebeia* colonies ceased to do so. This study also showed that *T. carbonaria* foragers spend over 30% of their foraging time hovering in close proximity to flowers, before finally alighting to collect pollen or nectar (Figure 3.7). Conversely, *A. australis* and *A. symei* spend over 90% of their foraging time exploring flowers and collecting pollen and nectar, while only 10% of their time is spent in flight between flowers.

Figure 3.7 *T. carbonaria* **forager hovering near a citrus flower. Photo: M. Halcroft**

3.4.2 *Austroplebeia:* adapted to the harsh Australian outback

Floral resources in the Australian outback are often unreliable. Regions may experience periods of drought that can last $1 - 4$ years (BOM, 2010b) (Figure 3.8). Alternatively, they can also experience occasional extensive flooding. Colonies of *Austroplebeia* have presumably evolved and adapted in order to survive such conditions. These behavioural adaptations ensure surviving nestmates exist within the colony after the drought has broken and a long-awaited floral bloom arrives.

Figure 8 Arid native range of *Austroplebeia australis*, Tara Queensland. Photo: M. Halcroft

Austroplebeia australis is an extremely long-lived worker bee, with a mean maximum worker longevity of 161.4 ± 6.1 days, and a maximum longevity of 240 days (Halcroft, unpublished data). The colonies forgo a 'high rate of living' when floral resources are unavailable. Only small numbers of foragers (4 returning / 2 min) are recruited during times of limited floral resources and whereas recruitment greatly increases (250 returning / 2 min) during floral abundance (A. Beil, personal communication; Halcroft, unpublished data). Colonies have also been observed closing their nest entrance with a resin curtain during periods of dearth (MH, personal observation; A. Beil, personal communication), presumably reducing the need to guard the nest entrance.

Many nest sites chosen by *Austroplebeia* are within dead trees (see Nest architecture), which provide no canopy protection against frosts in winter or searing heat in summer (Figure 3.9). While the insulation of natural logs is superior to that of most artificial hives, exposed trunks and limbs still allow temperature extremes to penetrate (R. Luttrell, unpublished data). Under such

circumstances, it might be expected that *Austroplebeia* has developed thermoregulatory mechanisms. This, however, is, not the case and studies have shown that *A. australis* brood temperatures parallel those of the empty nest cavity and the ambient conditions (Halcroft, unpublished data). Prior to the onset of the cold season, colonies begin constructing a layer of involucrum over the brood, on top of which honey pots are built and filled. Those structures provide some level of protection, as the brood beneath remains undamaged. Colonies that have not been prepared for cold exposure suffer chill damage and brood death (MH, personal observation). Brood can survive at temperatures as low as -1°C (although larval development is probably delayed) and as high as 38°C, indicating the possible development of physiological resistance to temperature extremes (Halcroft, unpublished data). *Austroplebeia australis* colonies do not become broodless during the cold winter months, although they build a smaller number of brood cells during this time. The bees may be stimulated to build brood during the winter months when the colony is artificially warmed and provided with supplemental food (Halcroft, 2007). *Austroplebeia australis*, and possibly other *Austroplebeia* species, have evolved in the unforgiving environmental conditions of arid inland Australia. Their ability to conserve energy through improved foraging efficiency and thermoconformity, and by reducing workers' exposure to high-risk activities and high rates of living, has resulted in a well adapted and resilient bee species. It is not only capable of surviving conditions most other species could not; it thrives in them.

Figure 3.9 Typical dead tree chosen by *Austroplebeia australis* colonies. Colonies in Tara, Qld, being sampled for further studies. Photo: S. Ruttley

3.5 The Australian stingless bee industry

(*Data pertaining to this section has now been published. See 'Article relating to my work' at www.beesbusiness.com.au)

The Australian stingless beekeeping industry is still very much in its infancy, especially when compared to many South American countries. However, comparative surveys conducted in 1998 (Heard and Dollin, 2000) and 2010 (Halcroft, unpublished data) show the industry is expanding and developing. Information provided below is based upon data compiled in 1998 and 2010.

In recent years there has been growing interest in Australian native bees, especially stingless bees. The honey and other hive products support an industry that has grown from 257 beekeepers in 1998, to 637 in 2010. Half of them owned just one hive and, in 2010, a quarter had less than 3 years of experience. The number of hives owned by the 637 beekeepers total almost 5,000. Over two-thirds of the beekeepers maintain their hives on suburban blocks, although many of them also live near some form of remnant natural vegetation or 'bushland'. The most commonly kept bees are *T. carbonaria, T. hockingsi, A. australis* and *A. symei.* In 2010, all but three survey respondents resided in New South Wales and Queensland.

Enjoyment and conservation were, by far, the most popular reasons for keeping stingless bees. The pollination of nearby vegetable and flower gardens, as well as bushland, was reported to be of considerable benefit. Only eight respondents provided pollination services on a professional basis (see Pollination).

3.5.1 Colony production

Australian stingless beekeepers use a variety of hive designs ranging from a simple, wooden box to a complex, insulated (or even heated), PVC-constructed, cylindrical hive. The most commonly used hive is based on the original Australian *Trigona* (*s.l.*) hive (OATH) design (Dollin, 2002; Klumpp, 2007) and has a capacity of 6 – 7 L. Most hives are constructed so that they can be

divided into two equal sections. Colony propagation techniques and hive design are discussed briefly here, because these topics are detailed elsewhere (Klumpp, 2007; Dollin and Heard, 2010; Heard, 2010).

Colony propagation of *Austroplebeia* is easier than for *Trigona* (*s.l.*). Small sections of brood containing a queen cell can be removed from an *Austroplebeia* colony and placed in a small hive, together with food stores and workers (A. Beil, personal communication; MH, personal observation). Queenright colonies with as few as 200 workers can survive and build strong colonies, if provided with the right conditions, which may include supplemental warmth and feeding (MH, personal observation). *Austroplebeia* colonies can also be strengthened during winter if maintained in artificially warmed rooms and provided with supplemental food (Halcroft, 2007). *Trigona* (*s.l.*) species, on the other hand, are more particular. Colonies need to be very strong before they are divided for propagation.

Propagation involves dividing the brood mass or inducing colony 'budding'. The quickest and, therefore, the most popular technique is 'splitting', and the success of a division is dependent upon the strength of the mother colony. Colonies (not including the hive or box) should weigh at least 2 kg or 3kg for those kept in the cooler southern regions (Klumpp, 2007). The hive, containing the brood and nest structures, is split horizontally into two sections, and the occupied sections are united with new, empty half-boxes (Heard, 1988a) (Figure 3.10). This results in two half-filled hives, one with a queen (mother colony) and one with several developing queen cells. Colony survival is dependent on adequate worker number for nest repair, foraging and defense, and the ability of the daughter colony to successfully 're-queen' (Klumpp, 2007).

Figure 3.10 Splitting OATH box with *T. carbonaria* colony. Photo: T.A. Heard

Colony budding is a non-invasive form of hive propagation. An empty hive is attached to the nest entrance of an existing colony via a black polyethylene pipe. This technique is often used when the nest is located in an inaccessible structure, such as a wall or living tree (Klumpp, 2007). An observation lid on top of the hive box is required to monitor progress of the 'budded' colony. The colony provisions the attached hive, and after several weeks or, more likely several months, a virgin queen leaves the colony and mates. If successful, she returns to the 'front hive' hive and begins laying eggs within several days. At the same time, the beekeeper intervenes by creating an opening in the connecting tube to allow foragers from the mother colony direct access to the nest. Eventually, the tube is disconnected or the bees close the connection themselves (Klumpp, 2007). This technique is ideal for those beekeepers who wish to increase their colony number but are not confident with the splitting technique. It does, however, require considerable patience.

The number of beekeepers involved in hive propagation has doubled. Those practicing hive division have increased colony number eight-fold since 1998. More than 8,000 colonies have been produced. The number of beekeepers who sell colonies has doubled, while the number of colonies sold each year has more than quadrupled. Although this development sounds impressive, the overall annual increase in colony number since 1998 is only 9% (Halcroft, unpublished data). The retail value of a strong stingless bee colony in Australia has increased from $AU200 to between $AU350-450 per hive. Demand is high and many producers report that they are unable to keep up with demand.

3.5.2 Australian stingless bee honey and other hive products

Honey harvesting techniques vary. Often pots are removed from the hive and honey is squeezed through a cloth or sieve. Beekeepers in Queensland and northern New South Wales, where bees can forage all year round, are able to harvest approximately 1 kg per year per hive. Beekeepers who reside in the cooler, southern regions are only able to harvest every 2 – 3 years, and almost not at all if they are in the Sydney basin or farther south (A. Ashhurst, personal communication, 2010). It is recommended that honey not be harvested if hive propagation is being practiced, because colonies require good stores to rebuild their strength (Dollin, 2002; Heard, 2010). Beekeepers who produce honey on a large scale utilize a honey super on top of hives. The OATH has a honey super with a capacity of 1.5 litres, and the following technique is used by Tim Heard and many other beekeepers.

The honey hive is fitted with a 'floorless' super that sits on top of a thin hive ceiling, which separates the main nest from stored honey (Figure 3.11). The separator provides access for the bees to all nest structures but still allows honey to be stored away from the brood. For easy, non-destructive honey harvest, the super is removed from the hive, exposing the intact pots (Figure 3.12). Excess pollen stored in the super is cut out before harvest, to reduce contamination and the

possibility of fermentation. The super is inverted and pots are pierced with a hand-tool similar to a small bed-of-nails. The super is placed over a plastic tray, into which fresh honey drains. After the honey is completely drained, the super is replaced and the bees can clean and rebuild the pots (Dollin, 2002; Heard, 2010). The only processing that occurs with sugarbag honey is straining out debris such as cerumen or bees.
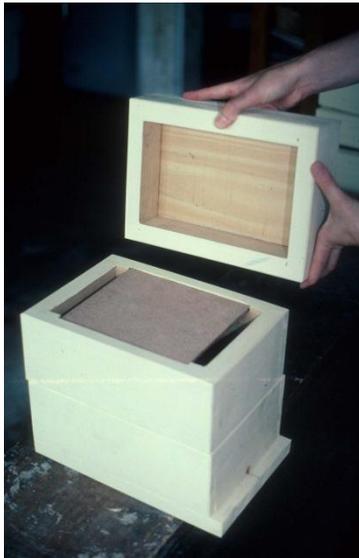

Figure 3.11 & 3.12 Honey super placed on top of OATH box, with separator in place. Photo: T.A. Heard, Honey super filled with honey, ready for harvest. Photo: M. Halcroft

Honey harvesting is carried out by a small number of Australian beekeepers and production is low. Although the number of beekeepers has more than doubled over the last decade, overall production of Australian sugarbag honey is < 300 kg per year. Of the 63 beekeepers who stated they harvest honey, only five reported selling their product, and they accounted for approximately half of overall production (Halcroft, unpublished data).

Sugarbag honey caters to a 'niche market' in Australia and its price is indicative of its rarity. The wholesale price has increased from $AU40 / kg in 1999 to $AU70 / kg in 2010; however, the retail price remains the same, approximately $AU160 / kg (Heard, 2010). In comparison, honey bee—*Apis mellifera*—honey sells for only $AU6.50 / kg (Shaw, 2010). Sugarbag honey is sold

in local markets, restaurants and via internet, and two producers export to Japan (Halcroft, unpublished data).

Limited research has been conducted on Australian stingless bee honey, but *T. carbonaria* has similar specifications to those of other Meliponine (Persano Oddo et al., 2008). Preliminary studies on antioxidant and antimicrobial activities have shown some promise for nutritional and pharmaceutical uses (Irish et al., 2008; Persano Oddo et al., 2008; Boorn et al., 2010). *Trigona carbonaria* honey has a moisture content of around 26% (Persano Oddo et al., 2008) and should be stored in the refrigerator to avoid fermentation (Heard, 2010).

The production of wax and resin supplies an extremely small market in Australia. Some beekeepers are able to sustainably harvest around 200g of cerumen per hive each year. It is sold to 'didgeridoo' manufacturers (see Introduction), artists and hobbyists, for $AU5 / 25g, which is sufficient to make up to four didgeridoo mouth pieces (Heard, 2010).

3.5.3 Pollination

Pollination of commercial crops by stingless bees is rare in Australia and growers of over 35 commercial crops rely heavily on managed honeybee colonies (RIRDC, 2007). Free pollination services are also provided by colonies of feral honeybees in Australia, with 40 - 150 colonies / km^2 present in some surveyed areas (Oldroyd et al., 1997). The Australian honeybee pollination industry is currently strong and reliable (RIRDC, 2007); therefore, little funded research has been undertaken on native bees as alternative pollinators. However, the reliability of the honeybee industry is now in question because, managed and feral bee populations are declining due to pests and disease, as well as possible pesticide problems. For example, between 2002 and 2006 more than 4,500 colonies died out due to African small hive beetle *Aethina tumida* Murray (Nitidulidae) infestation (Rhodes and McCorkell, 2007). Australia is the only major country without varroa mite *Varroa destructor*, but the likelihood of an incursion has raised major

concerns about the future reliability of the honeybee pollination industry in this country (RIRDC, 2007).

A rapidly-expanding almond *Prunus dulcis* (Rosaceae) industry in Australia has resulted in industrial migration of thousands of managed honeybee colonies, transported in from the northern regions for their pollination service. It is estimated that the almond industry requires one-half of all managed honeybees in the eastern states of Australia (RIRDC, 2010). This continued development, together with the predicted overall reduction in colony number, is likely to stimulate increasing interest in alternative pollinators in the warmer regions of northern New South Wales and Queensland, from which many honeybee colonies will be taken. There is already a small group of stingless beekeepers that provide pollination services in these regions. The Australian stingless bee pollination industry had its beginnings in the late 1980s when it was found that yields of macadamia nut *Macadamia integrifolia* (Proteaceae) grown near remnant native vegetation were noticeably higher than for crops situated in cleared land (Heard, 1988a; Heard and Exley, 1994). The main pollinators of macadamia are honeybees and stingless bees (Vithanage and Ironside, 1986), and presence of these insects is extremely important for maximum seed set (Wallace et al., 1996). Although the temperature threshold for *Trigona* (*s.l.*) flight activity is 18°C (Heard and Hendrikz, 1993), resulting in shorter foraging days compared to honeybees (7 hours vs. 10 hours per day, Heard and Exley, 1994), *Trigona* (*s.l.*) are superior pollinators of macadamia flowers. Their small bodies are able to make more intimate contact with stigmata while collecting pollen (Heard, 1994), thus aiding pollen transfer.

Trigona carbonaria are opportunistic foragers that use group strategies to independently search for resources, and rapidly recruit nest mates once rewards are located. Foragers demonstrate floral constancy (White et al. 2001) and resources are harvested, often by groups of bees, until they are depleted (Bartareau, 1996). Few studies have been carried out on Australian stingless bee communication. Bartareau (1996) reports that *T. carbonaria* foragers leave a marker of

glandular secretions near the food resource, but do not leave scent trails from the resource to the nest (Nieh et al.2000). Heard (1987) also demonstrated that *Trigona* (*s.l.*) foragers returned to hives with 100% macadamia pollen, compared to honeybees, carrying only 24%. Interestingly, *Trigona* (*s.l.*) prefer warm flowers (Norgate et al., 2010) and this is demonstrated by their attraction to flowers on outer, sun drenched racemes (Heard and Exley, 1994). Macadamia also benefit from varietal interplanting for cross pollination (Rhodes, 1986) as their flowers are mostly self-incompatible and protandrous (providing pollen before stigmata are receptive) (Sedgley et al., 1985).

Heard (1988b) developed a technique whereby colonies could be transferred into artificial hives for use in managed crop pollination. The use of stingless bees for pollination of macadamia has grown since then, and several macadamia farmers have purchased their own hives to improve crop yield. Some growers were originally honeybee keepers, but found it easier to move small *Trigona* (*s.l.*) hives to their macadamia crops, which are often grown on steep slopes. Those farmers have since become reputable stingless beekeepers in their own right (F. Adcock, personal communication). The demand for stingless bee pollination service by the macadamia nut industry, as well as other crops, is growing. At present, there are not enough hives available to meet this demand (M. Grosskopf, personal communication, 2010). Further effort is required to improve colony propagation. This would ensure that enough colonies are available in the future for suitable stocking rates and satisfactory pollination service (T. Carter, personal communication).

It is estimated that Australian stingless bees have an average flight range of only 500 m (Heard and Dollin, 1998). This is advantageous for crop pollination, because bees are more likely to forage within the crop area than to venture farther afield in search of other floral resources, as is often the case with honeybees (Graham, 1992). Hive placement is important, and the 15 – 20 hives per hectare (compared to seven honeybee hives per hectare) should be interspersed

throughout the crop if possible, especially if cross-pollination is required (Heard and Dollin; F. Adcock, personal communication; T. Carter, personal communication).

Crops other than macadamia can also benefit from stingless bee pollination. Anderson et al. (1982) showed stingless bees to be effective pollinators of mango (*Mangifera indica;* Anacardiaceae) and anecdotal accounts of increased crop quality and yield have been reported for other crops such as lychee *Litchi chinensis* (Sapindaceae), avocado *Persea americana* (Lauraceae) and watermelon *Citrullus lanatus* (Cucurbitaceae) (T. Carter, personal communication). Although no scientific studies have been conducted on the effectiveness of stingless bees as pollinators in Australian crops other than macadamia and mango, estimates of improved crop yield have been assessed by one beekeeper. Stingless bees have also been introduced into blueberry (*Vaccinium corymbosum;* Ericaceae) and bees are able to collect pollen and nectar more efficiently than honey bees (F. Adcock, S. Maginnity, M. Grosskopf, personal communication). Blueberry flowers are small, with a deep corolla and narrow terminal orifice (Rhodes, 2006). Unfortunately, there is no experimental design or statistical analysis associated with these trials. Although the role of stingless bees in pollination of native flora is well documented, their efficacy in horticultural and agricultural crops of Australia needs further study (Heard, 1987; Heard, 1999; Slaa et al., 2006).

Of the eight beekeepers who reported that they provided pollination services on a professional basis during 2010, only four charged a service fee. One beekeeper charged only $AU10 per hive, while the other three charged $AU35 – 40 per hive (Halcroft, unpublished data).

3.6. Management issues

3.6.1 Pests of Australian stingless bees

Australian stingless bees seem to be relatively disease-free and no reports of brood disease have been seen. They do, however, suffer from predation, parasitism and colony infestation. There are

many general predators such as flies, ants, spiders, mites, wasps, birds, lizards, toads and, of course, humans, which are common pests of social bees worldwide. Australia has its own unique species of stingless bee parasites and predators; however, little is known about most species. Usually, strong hives are at minimal risk of hive invasion but weakened or newly propagated colonies are vulnerable to attack from pests. It is of critical importance, when managing colonies, that all means of access to the nest cavity are well sealed and that colonies are divided or transferred as quickly and efficiently as possible, to minimize pest infestation.

One of the most serious pests of stingless bee colonies in Australia is the syrphid fly *Ceriana ornata australis* Macquar. *Ceriana ornata* is 12mm long, with bright orange-yellow and black markings (Figure 3.13) and is frequently observed hovering near nests during summer (MH, personal observation). This fly has been observed in all regions where stingless bee colonies are present and is seldom observed in areas where stingless bees do not occur (Klumpp, 2007). *Ceriana ornata* is most destructive when colonies are divided or damaged. The female lays eggs directly on nest structures if the hive is left open and unattended, or eggs are laid in unsealed joints or cracks in the hive surface. The eggs hatch and the larvae (Figure 3.14) make their way into the nest cavity and food stores. If fly larval numbers are high the colony will die as stores and immatures are consumed.

Figure 3.13 Syrphid fly adult. Photo: J. Klumpp

Figure 3.14 Syrphid fly larvae in nest of dead colony. Photo: M. Halcroft

The phorid fly *Dohrniphora trigonae* Disney can also cause problems in Australian stingless

bees, especially *Trigona* (*s.l.*) species (Disney and Bartareau, 1995). Similar to phorid fly pests

overseas (genus *Pseudohypocera*), *D. trigonae* lays its eggs within the colony stores and are most problematic following colony division (Klumpp, 2007; Dollin and Heard, 2010). These tiny flies (2.5 mm) (Figure 3.15) enter nests more easily than the larger syrphid fly, and can do so in high numbers (Klumpp, 2007). Once inside, flies run along the surface of the structures, laying eggs in honey and pollen pots. This pest is less of a problem in Australia than overseas.

Figure 3.15 *Trigona* worker (*left*) beside a phorid fly (*right*). Photo: J. Klumpp

Stingless bee predators that are unique to Australia include *Bembix flavipes* Smith and *Bembix musca* Handlirsch (Crabronidae) (Figure 3.16). These *Bembix* hunt singly and hover outside the entrance, waiting for bees to exit. Once a bee leaves the nest the wasp swoops from behind the unsuspecting worker and drags it to its own nest (A. Beil, personal communication, 2009). Evans et al. (1982) observedmass provisioning of *B. flavipes* nests with over 25 freshly collected *Austroplebeia,* and *B. musca* provision nests with *T. carbonaria*. Drones are the main prey during the stingless bee mating season (Evans and O'Neill, 2007).

Figure 3.16 *Bembix* **wasp. Photo: J. Klumpp**

The only know parasitoid of Australian stingless bees is the braconid wasp (*Syntretus trigonaphagus*) (Gloag et al., 2009). *Syntretus trigonaphagus* has only been reported in the Brisbane area. The distribution of its host, *T. carbonaria*, suggests that it may be found more widely along the east coast of Australia. Wasps wait near the hive entrance or on flowers where bees are foraging (Figure 3.17). When close enough to the posterior of an individual bee the wasp projects her abdomen under and in front of hers and oviposits onto the abdomen of the bee. The hatching larva grows inside the abdomen of the living bee, for an unknown period of time. Parasitised bees are easily identified because the abdomen is 2 – 2.5 times larger than that of normal bees. The fully-developed larva emerges from the bee, which then usually flies away, presumably to die. Gloag et al. (2009) were unable to successfully rear pupae from emerged larvae and it is thought that pupation may take place in the soil (Klumpp, 2007).
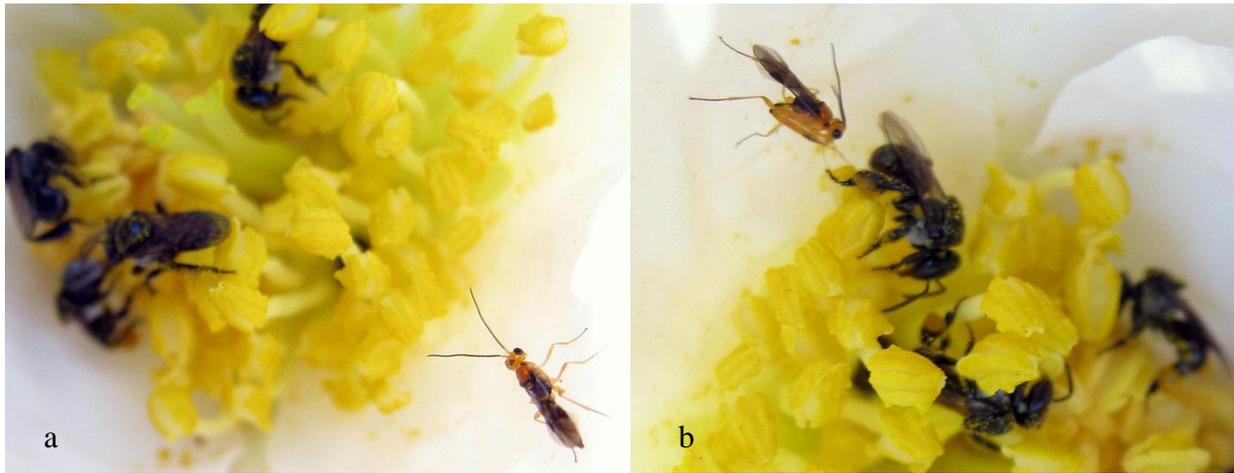
Figure 3.17 (a) Braconid wasp (right) lying in wait near Trigona foragers. (b) Braconid wasp (left) preparing to oviposit into Trigona forager. Photos: J. Klumpp

Australian native beetles in the genus *Brachypeplus* (Coleoptera: Nitidulidae) have been observed in stingless bee hives (MH, personal observation) although it is thought they are not a major problem for strong colonies (A. Dollin, personal communication, 2010). Adult beetles are commonly observed on the outer surfaces of hives. These beetles are smaller and more slender than the worker bees (Figure 3.18) and are, therefore, able to gain access through unsealed cracks and joints in hives. They lay eggs in inaccessible cracks and crevices within the hive. Beetle larvae have not been observed in high numbers within hives and the main signs of their presence are the accumulation of dry debris in the bottom of the hive, and a reduction in worker bee number (MH, personal observation). Little is known about these native beetles and it is unclear what the larvae consume within the stingless bee nests. Pupating beetle larvae have been observed under the transparent lid of *A. australis* hives, indicating that these beetles can complete their life cycle within the nest (MH, personal observation).

Figure 3.18 Adults and larva of *Brachypeplus* sp. beside an *Austroplebeia australis* worker. Photo: M. Halcroft

Figure 3.19 Adult small hive beetles beside an *Austroplebeia australis* worker. Photo: M. Halcroft

The African small hive beetle (*Aethina tumida* Murray; Nitidulidae) is a newly introduced honey bee pest in Australia (Figure 3.19) and can devastate newly divided, or damaged, stingless bee colonies. Adult beetles are frequently found near hives (MH, personal observation) and enter nest openings whenever possible. If left unchallenged, the beetle lays eggs in food stores and brood. The larvae hatch and begin feeding, defecating throughout the nest, and cause hive contents to ferment. Eventually the entire colony collapses into a slimy mass. As with syrphid fly invasion, strong colonies are usually able to remove larvae from an infested nest, but prevention is always better than cure. A strong, undamaged colony can defend against small hive beetle invasion, and studies have shown that *T. carbonaria* can incapacitate invading adult beetles

within 10 minutes of being introduced to the nest entrance (Greco et al., 2010). Halcroft et al. (2011) showed that *A. australis* was effective in removing or destroying all life stages (eggs, larvae and adults) from hives and that efficiency in entrance defence and invader removal increased with frequency of exposure to beetle invasion. Both *T. carbonaria* and *A. australis* utilize resin to entomb adult beetles within the nest (Figure 3.20). *Austroplebeia australis* later dismembers the remains and removes them from the nest.

Figure 3.20 Adult small hive beetle entombed alive in cerumen while an *Austroplebeia australis* worker guards the interloper. Photo: M. Halcroft

Another exotic predator of Australian stingless bees is the cane toad (*Rhinella marina—*formerly known as *Bufo marinus* Linneaus; Bufonidae). Introduced into Australia in 1935 as a biological control agent for the pest cane beetle this highly toxic pest has spread from coastal northern Queensland to the central coast of New South Wales, and across northern Australia to Kakadu National Park in Northern Territory (Australian Museum, 2010). Cane toads are quite ingenious and may stand on each other's backs in order to reach bee hive entrances. The toad will stay at the hive entrance and consume incoming and outgoing workers until forager numbers dwindle, to the point that the colony may be in danger of perishing (R. Zabel, personal communication) (Figure 3.21).

Figure 3.21 Cane toad waiting at the entrance of a stingless bee hive. Photo: R. Zabel

3.6.2 Seed dispersal by stingless bees

Corymbia torelliana F. Mueller (Myrtaceae), or cadaghi tree, as it is commonly known, is native to the rainforest margins of the Atherton Tablelands in northern Queensland. This species of Australian gum tree has spread extensively outside its native range as it has been used for plantation timber. Its abundant blooms (Figure 3.22) and showy gum nuts (Figure 3.23), have also resulted in it being used in street plantings and parks, especially in the Brisbane area (AWC, 2010). Although it is a source of abundant pollen and nectar in spring, it has become a major management problem for some stingless beekeepers.

Figure 3.22 *Corymbia torelliana* **flowers are an abundant pollen and nectar source. Photo: J. Klumpp**

Figure 3.23 The attractive gum nuts of *Corymbia torelliana* **make it an ideal amenities tree. Photo: J. Klumpp**

Corymbia torelliana seeds are mainly dispersed by gravity; 88% of seeds drop to the ground soon after the fruit opens. However, one or two seeds remain within the gum nut and all are dispersed by *Trigona* (*s.l.*) (Wallace et al., 2008). Resin is produced in the gum nut, behind the valve (Figure 3.24). When the bee enters the nut to collect resin, the seeds attach to the sticky corbicular load (Figure 3.25). Seeds are dispersed by bee vectors, or 'mellitochory', and may be spread during the flight back to the nest or transported to the nest itself. This may be up to 1 km away from the tree (Klumpp, 2007; Wallace et al., 2008; A. Beil, R. Luttrell, J. Klumpp, personal communication). *Trigona* (*s.l.*) are strongly attracted to the resin from *C. torelliana* and the colonies stop normal foraging activity to collect as much of this resource as possible (Klumpp, 2007). *Trigona* (*s.l.*) are known to collect and store large amounts of resin, with up to 10% of foragers returning with resin loads (Wallace and Lee, 2010). Analysis of the chemical profiles of body surfaces of five *Trigona* (*s.l.*) species showed that 51% of these compounds were derived from plant resins. Conversely, *Austroplebeia*, which collect only small amounts of plant resin, had little or no resinous compounds on their bodies (Leonhardt et al., 2010).
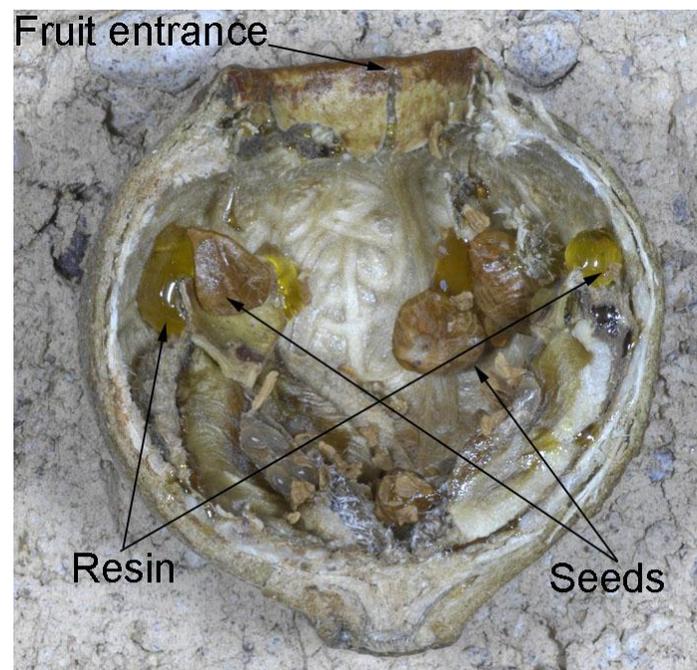

Figure 3.24 Cross section of *C. torelliana* fruit, showing seeds and resin in close proximity. Photo: R. Luttrell

Figure 3.25 *Trigona* **forager on** *a C. torelliana* **fruit, with a seed adhered to her corbicular load. Photo: R. Luttrell. Figure 3.26** *C. torelliana* **seed collection around the entrance of a** *Trigona* **nest entrance. Photo: R. Luttrell**

As foragers return to the nest some attempt to dislodge seeds on the nest exterior, while others transport seeds directly into the nest cavity. The colony removes some, but not all, of the introduced seeds and these are either disposed of, up to 10m outside the nest (Wallace and Trueman, 1995), or adhere to the sticky surface of the nest entrance (Wallace et al., 2008) (Figure 3.26). Seeds collect around the entrance (Wallace and Trueman, 1995), reducing airflow within the nest. Resin from *C. torelliana* may have a lower melting point than many other plant resins. Collection of the resin and its seed occurs during the hottest months of the year in Australia — December to February (Wallace and Lee, 2010), and as temperatures rise, the resin begins to soften. Reports of structural collapse due to seed weight and resin softening are not uncommon, particularly if ambient temperatures exceed 39°C (J. Klumpp, M. Duncan, personal communication, 2006). As a result, some beekeepers remove their hives from *C. torelliana* areas during resin flow to prevent colonies from collecting the resin and seed mixture (Klumpp, 2007; T. Carter, personal communication, 2010). While many Australian beekeepers consider *C. torelliana* to be a major management problem, others consider it to be a useful source of pollen, nectar and resin (Klumpp, 2007).

3.6.3 Fighting swarms

Nest defence is widely reported in stingless bees around the world. Incapacitation of intruders is achieved by biting, resin daubing, chemical repellents and locking onto the wing or body with their mandibles, thus grounding invaders and rendering them harmless (Roubik et al., 1987; Wittman et al., 1990; Lehmberg et al., 2008; Halcroft et al., 2011). Nest defence against conspecifics is, however, more specialized and involves recognition of nestmates from non-nestmates, using recognition cue compounds (Buchwald and Breed, 2005). *Trigona carbonaria* demonstrate a collective defence behaviour known as a 'fighting swarm', during which time hundreds to thousands of workers, usually from two colonies, become entwined in an aerial battle, to the death. The fight takes place outside the defending nest and may result in the usurpation of the defending colony. In flight, two workers lock together by biting each other, and immediately drop to the ground. Sometimes the opponents mistakenly attack their own nestmate and, once they recognise this, the pair will usually unlock mandibles and take to the air again, rejoining the fight. Typically, the combatants remain locked together until death, after which they are dragged away by opportunistic scavengers, such as ants. The battle, which may begin each morning and can last for days, results in a carpet of thousands of dead, bees locked together by the mandibles (Figure 3.27) (Wagner and Dollin, 1982; Heard, 1996; Klumpp, 2007; Dollin, 2008; Gloag et al., 2008).

Figure 3.27 T. carbonaria hive entrance showing just a proportion of the coupled bees that will die in battle. Photo: R. Gloag

Gloag et al. (2008) found that most 'fighting swarms' involved only two colonies. However, there were instances where up to seven colonies were identified in a single battle. Alarm pheromones are probably responsible for attracting neighbouring colonies into the 'fighting swarm'. This may potentially increase overall losses within a meliponary or orchard. *Trigona carbonaria* is the most popular species kept by Australian stingless beekeepers (Halcroft, unpublished data), and 'fighting swarms' are a major management problem. While there are reports of other stingless bee species forming defensive groups, 'fighting swarms' are regularly reported in *T. carbonaria* (ANBees, 2010). Colony strength is greatly reduced after a fight and colonies may not be divisible for another season. Gloag et al. (2008) also find that approximately one in five of the paired combatants were nestmates, contributing further to the cost of battle.

Gloag et al. (2008) tested the theory that returning workers may become disorientated, especially when moved into a crop area for pollination. Workers were forced to enter a foreign nest, which quickly provoked a 'fighting swarm'. In the field, disoriented workers mistakenly entered another nest, thus prompting a 'fighting swarm'. Management practices that are used to reduce the incidence of 'fighting swarm' due to disorientation include: separation of hives by 5 m, positioning hives at different heights and directions, and identification of hives with different colours or symbols (Gloag et al., 2008). Fortunately, colonies involved in 'fighting swarms' usually recover (Heard, 1996) and in the case of usurpation, the weaker colony may even increase in vigour (Dollin, 2008).

More information on fighting swarms can be found at http://www.aussiebee.com.au/video-fighting-swarms-1.html

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