

# Chapter 11

## Use of Plant Resins for Defense and Nest Building in Stingless Bees



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### 11.1 Introduction

Pollen and nectar are the primary rewards sought by bees; however, more than 30% of bee species depend on nonfloral resources to provision their brood cells or to construct and defend their nests (Simpson and Neff 1981; Roubik 1989; Requier and Leonhardt 2020). In the case of stingless bees, nonfloral resources collected by foragers include soil, mud, feces, fungal spores, seeds, and resin, the latter often in large quantities (Roubik 1989). Resins are mixtures of terpenoids and/or phenolic compounds produced by plants, secreted both in internal structures or on the surface of the plant (Langenheim 2003). For stingless bees, the resin is as vital a resource as pollen and nectar. Such is the importance of resins that many species collect the sticky substances in groups and show threat displays or aggressive behaviors (e.g., air collisions, body-to-body fighting) to defend resin production sites (Howard 1985; Reyes-González and Zamudio 2020). Resin is obtained from a great diversity of plants, and stingless bees can use it in different ways, for example, to make

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cerumen (a mix of wax and resin, see below), which is the principal material used in the construction of their nests (Wille and Michener 1973). Meliponines can also use resins to defend their colonies or themselves against enemies or intruders (Wille 1983; Sakagami et al. 1993; Grüter et al. 2016), and, in some species, they may be involved in nestmate recognition (Leonhardt et al. 2009). Additionally, resins protect the nest against infections caused by viruses, bacteria, yeasts, and fungi (Langenheim 2003).

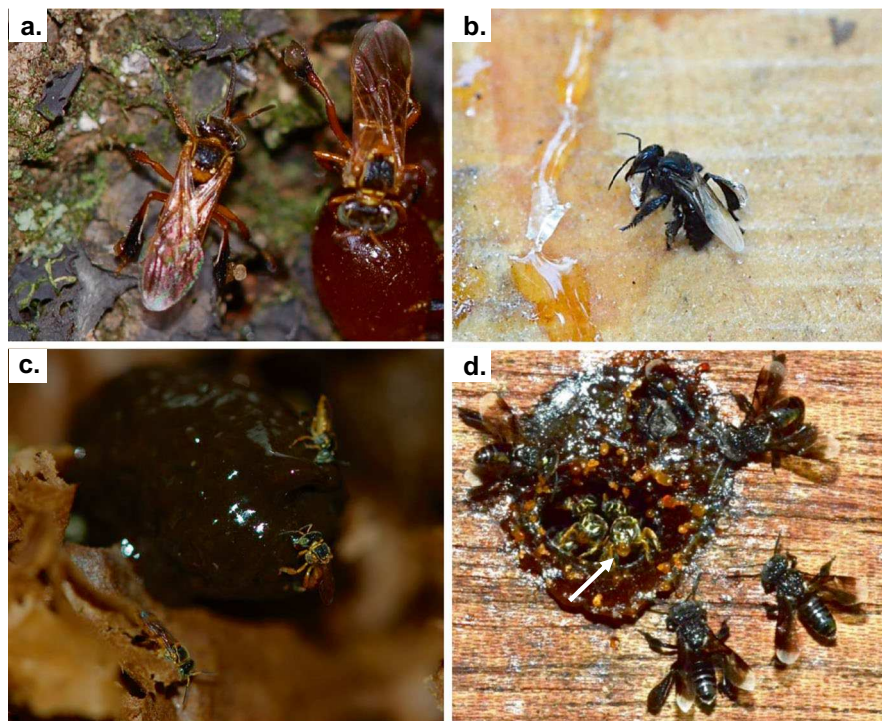
## 11.2 Resin Handling

Resin collection is mainly performed by the worker bees (Bassindale 1955; Roubik 1989; Hammel et al. 2016). Although there are records of males of a few species (e.g., *Tetragonula fuscobalteata*, *T. pagdeni*, *T. collina*, *Heterotrigona apicalis*) carrying resin on the hind legs, males do not play a significant role in resin foraging since they never deposit their loads on resin piles within the nest as workers do (Boongird and Michener 2010). Stingless bees collect resin from a wide range of plant species (Roubik 1989; Leonhardt and Blüthgen 2009; Wallace and Lee 2010; Drescher et al. 2014), where it is secreted by leaves, wood, flowers, fruits, and bark, often in response to plant injuries or infections (Roubik 1989; Langenheim 2003) (Fig. 11.1a). Some *Trigona* workers bite plant parts to stimulate resin secretion, and this can stimulate resin flow for days (Wille and Michener 1973).

When a foraging worker discovers a resin source, it uses the tips of the mandibles to form a ridge on the surface. At first, the resin is trimmed and transferred from the mandibles to the pretarsi of the front legs (Fig. 11.1b), then to the basitarsi of the middle legs and finally, to the corbiculae of the hind legs where the load is carried to the nest (Schwarz 1948; Bassindale 1955; Gastauer et al. 2011) (Fig. 11.1b). Once inside the nest, foragers unload and deposit the resin on piles (Fig. 11.1c) or in storage pots, sometimes helped by their nestmates (Gastauer et al. 2011). They use the mandibles to remove the resin from the hind legs of the returning foragers and to carry the load inside the nest (Gastauer et al. 2011). In the case of an unaided unloading, the returning worker brushes the resin top-down from the corbiculae, using the tarsi of the middle legs, to drop it into the pot or on the pile (Bassindale 1955; Gastauer et al. 2011). Afterward, the residual resin stuck to the tarsi of the middle and hind legs is cleaned by rubbing tarsi one against another (Gastauer et al. 2011).

Besides the transportation of resin from the natural source to the nest, bees carry and deposit resins inside the nest, for example, between the storage sites and a construction site or to the entrance to defend the colony against an intruder. For that purpose, the resin is held by the tips of the mandibles and fixed beneath the workers' head. Once at its destination, the bee attaches the resin to the target (i.e., construction site, intruder) and opens its mandibles to deposit it there (Fig. 11.1d) (Gastauer et al. 2011).

Resins are secreted as liquids but they harden over time (Armbruster 1984; Roubik 1989). How stingless bees handle resins without harming themselves or



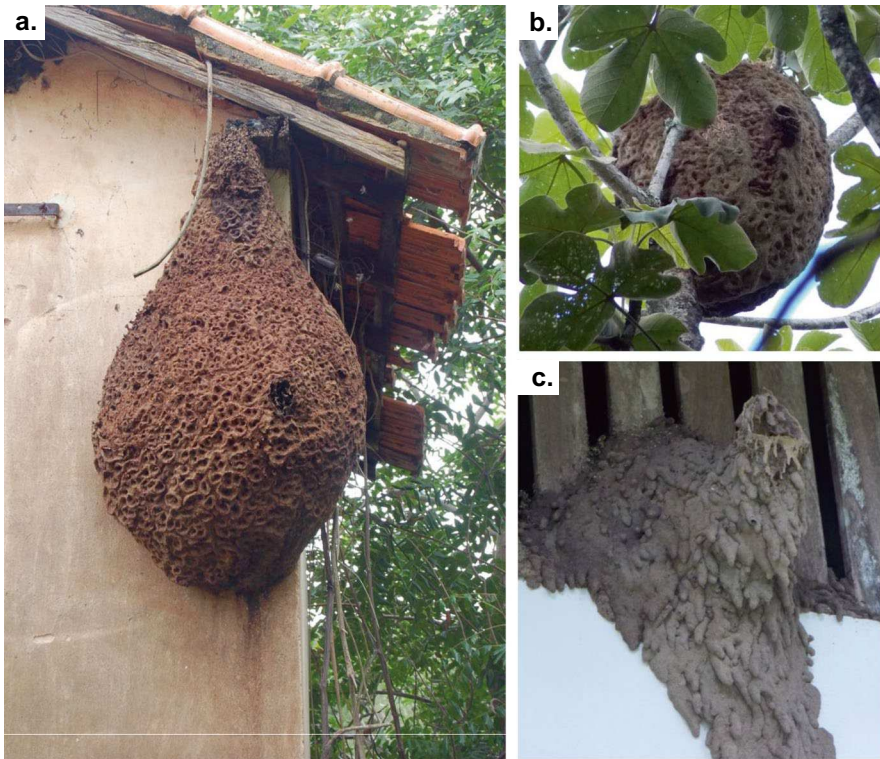
**Fig. 11.1** Handling of resins. (a) *Frieseomelitta varia* collecting resin from a tree. (b) *Trigona hyalinata* transferring resin from their mandibles to the front legs. (c) *Tetragonisca angustula* workers on resin pile. (d) *Plebeia droryana* carrying a resin ball with its mandibles (white arrow), in response to a *Frieseomelitta languida* raid. (Photos: Christoph Grüter)

getting stuck in them is not fully understood. Some studies propose that, given that the tarsi and corbiculae of *Tetragonisca angustula* do not show physical antiadhesive properties (i.e., specialized surface structures) against resin, they might lubricate their mandibles to reduce resin's adhesion (Gastauer et al. 2013). These putative lubricating substances could be secretions from the mandibular and head salivary glands, as known for *Plebeia emerina* to maintain the consistency of stored resin (dos Santos et al. 2009). Some studies show that in *Hypotrigona gribodoi*, *P. emerina*, and *T. angustula* resin manipulation is age-related and is performed by older workers (Bassindale 1955; dos Santos et al. 2010; Hammel et al. 2016). In *P. emerina*, this might be related to the development of the cephalic glands mentioned above (dos Santos et al. 2009). Other species collect floral resins, which remain liquid for several weeks after secretion (Armbruster 1984). Thus, workers can gather and store them within the nest for a long time (Roubik 1989). Such is the case in several species of *Trigona* who collect resin from *Dalechampia* (Euphorbiaceae) and *Clusia* (Clusiaceae) flowers (Armbruster 1984). Although almost all meliponines use resins, further investigation is needed to better understand how bees prevent being trapped when collecting resin.

### 11.3 Resins in Nest Construction

Unlike most other bees, meliponines build perennial nests (Michener 2007; Roubik 2020; Grüter 2020). In general, stingless bees prefer an existing cavity to settle their colonies. Although the cavity is usually found in a tree, nests are sometimes located underground (Roubik 2006). In some cases, the site chosen was previously occupied by other social insects such as termites and ants (Schwarz 1948; Bassindale 1955; Roubik 1983; Wille 1983; Camargo and Pedro 2003; Grüter 2020). In contrast, some species of the genera *Trigona*, *Partamona*, *Paratrigona*, *Dactylurina*, *Plebeia*, and *Tetragonisca* build fully or partially exposed nests attached to tree branches or trunks, lianas, or buildings (Schwarz 1948; Michener 1964; Wille and Michener 1973; Wille 1983; Roubik 1983, 2006; Camargo and Pedro 2003; Rasmussen and Camargo 2008; Grüter 2020) (Fig. 11.2).

Most nest structures are made of wax secreted by workers mixed with materials they collect from the environment, such as resins, gums, mud, and feces (Schwarz 1948; Wille and Michener 1973; Wille 1983; Michener 2007). Cerumen, a mixture of bee wax and resin, is the principal nest construction material (Camargo 1970;

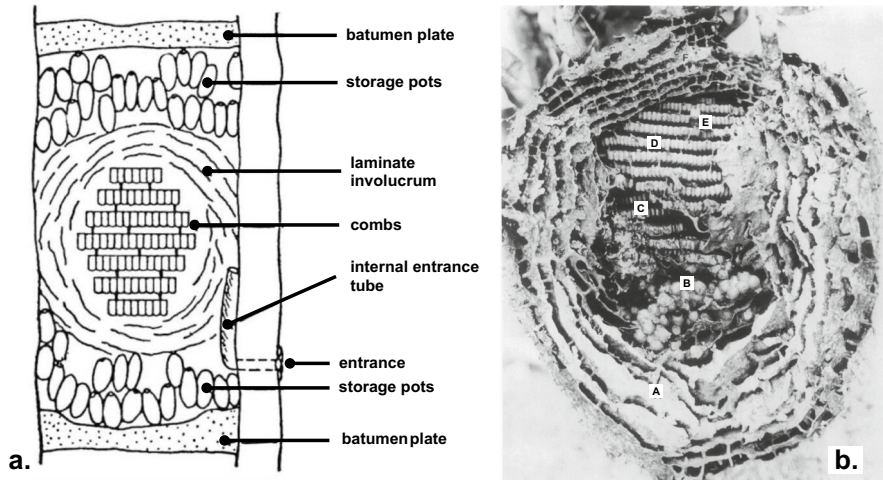


**Fig. 11.2** Exposed nests of: (a) *Trigona hyalinata*, (b) *Trigona spinipes* in a tree (Ribeirão Preto, Brazil), (c) *Partamona* sp. (Belem, Brazil). (Photos: Christoph Grüter)

Wille and Michener 1973; Wille 1983; Shanahan and Spivak 2021). Stingless bees use it to build brood cells, the involucrem (soft cerumen sheets that protect the brood cells in many species), nest entrances, pillars, or storage pots (Schwarz 1948; Roubik 1989, 2006). In ground nesting species, like *Geotrigona* or *Schwarziana*, cerumen is used to build furrows in the involucrem that are thought to prevent water from entering the brood nest (Roubik 1989). Depending on the proportions of wax and resin, cerumen can be a soft and light brown material (containing more wax than resin) or rigid, brittle, and dark brown or black (more resin than wax) (Wille and Michener 1973). Moreover, the relative amounts of resin and wax used in cerumen differ among species and nest structure (Schwarz 1948; Roubik 2006). For example, Blomquist et al. (1985) found that the small bees of the genus *Trigonisca*, which nest in stems, use almost pure wax. In the case of the Amazonian stingless bee *Scaura* (formerly *Schwarzula*) *coccidophila*, all parts of the nests, including brood cells, storage pots, and the entrance tube, are built with pure wax (Camargo and Pedro 2002), while in other species the resin can represent 30–40% of the cerumen (Schwarz 1948). This unusual species does not appear to collect or use any resin, which (if true) could be due to their mutualistic relationship with wax-producing scale insects which provide the bees with large amounts of pure wax (Camargo and Pedro 2002).

Nests are usually surrounded by one or several layers of wax mixed with larger amounts of resin and/or mud, the batumen (Schwarz 1948; Michener 1964; Wille and Michener 1973; Grüter 2020). In the case of nests in cavities, the major nest walls of batumen often delimit the portion of the hollow used for the nest (Michener 1964; Camargo 1970; Camargo and Pedro 2003; Roubik 2020). Most commonly they consist of batumen plates closing off portions of a natural cavity from the nest cavity, and lining batumen (thin layer of batumen, rarely partly mud) on the walls of the nest cavity (Fig. 11.3a) (Wille and Michener 1973). When nests are partially or fully exposed (e.g., *Partamona*, *Trigona*), batumen consists of several layers with airspaces between them, creating an insulating and protective barrier (Michener 1964). In some cases, this multilayered batumen can be 10–20 cm thick, encasing the whole nest except for the entrance hole (e.g., *Melipona*, *Trigona corvina*) (Michener 1964; Wille and Michener 1973; Roubik 2006) (Fig. 11.3b). The exposed nests of some species of the genus *Trigona* (e.g., *T. spinipes*, *T. corvina*, *T. nigerima*, *T. amalthea*) present an outer layer containing plant materials (e.g., chewed leaves, fibers), or dung of herbivorous animals, pollen exines or bee feces, surrounded by thin layers of batumen, sometimes called a scutellum (Nogueira-Neto 1962; Wille and Michener 1973; Roubik 1983, 2006). These layers outside of the scutellum are easily broken by a predator attack, causing the release of many defending bees. In the case of *T. spinipes*, bees open holes in the outer nest shell in response to temperature and ventilation needs, thus the thin shell may serve more than one function (Roubik 2006).

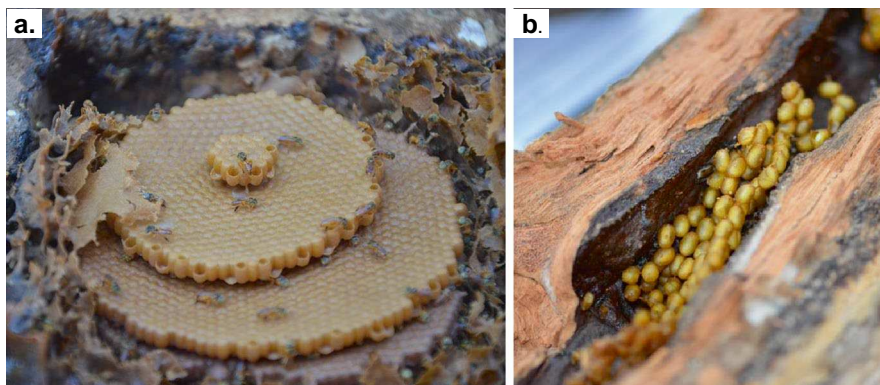
Within the nests, the brood chamber is usually enclosed by soft layers of cerumen called the involucrem (Fig. 11.3), which serves as a protective sheath for the brood and helps maintain an adequate temperature for their development (Schwarz 1948; Michener 1964; Camargo 1970; Wille and Michener 1973; Roubik 2006;



**Fig. 11.3** Nest structure. (a) Diagram showing the structures of a stingless bee nest with horizontal and spiral brood combs. (From Nogueira-Neto 1997). (b) Details of a *Trigona nigerrima* nest architecture. (From Roubik 1983). A: scutellum, B: storage pots, C: brood cells, D: pupal cells, E: queen cell, F: laminate batumen

Grüter 2020). In some species, the involucrum is incomplete or absent and this seems to be related to the climatic conditions (e.g., *Plebeia poecilochroa*, *P. remota*, *P. julianii*) (Camargo 1970; Drumond and Melo 1995). Species that nest in environments where the temperature is high and relatively uniform do not need to strongly regulate the temperature inside the brood chamber (e.g., *Tetragona dorsalis*, *Melipona amazonica*, *M. interrupta*) (Camargo 1970). The absence of an involucrum is also related to the place where the nest is built. The species that construct the nest inside active ant or termite nests need no involucrum, since the temperature is uniform due to the presence of the hosts (e.g., *Trigona cilipes*, *Scaura latitarsis*) (Camargo 1970). Furthermore, the involucrum is absent in the nest of almost all species whose brood cells are irregularly arranged (clusters) (e.g., *Hypotrigona*, *Leurotrigona*, *Trigonisca*, and *Frieseomelitta*), presumably as an adaptation to nesting in restrictive spaces, since a nest organized into combs surrounded by an involucrum could not possibly be accommodated in small, narrow, and irregular spaces (e.g., crevices in logs) (Fig. 11.4) (Michener 1964; Camargo 1970; Wille and Michener 1973; Grüter 2020). Alternatively, *Austroplebeia australis* and *Plebeia remota* construct and deconstruct the involucrum according to seasonal changes, expanding the involucrum during the coldest months of the year, while in summer it is absent or consists of only a thin layer (van Benthem et al. 1995; Halcroft et al. 2011).

Finally, both the brood cells and storage pots (honey and pollen pots) are made of soft cerumen (Wille and Michener 1973). In species that have an involucrum, the storage pots are inside of the batumen and outside of the involucrum (Wille and Michener 1973). Additionally, pillars of soft cerumen connect the brood cells



**Fig. 11.4** Comb organization. (a) Horizontal brood combs of *Tetragonisca fiebrigi*, (b) Clustered brood cells of *Frieseomelitta languida*. (Photos: Christoph Grüter)

(clusters or combs) with each other and with the surrounding structures (Wille and Michener 1973; Wille 1983). Moreover, pillars connect all nest structures with the batumen and those located on the bottom of the nest are thickened and brittle (Wille and Michener 1973).

In sum, the addition of resin provides several benefits that allow stingless bees to nest in wet environments such as the tropics: (i) resin is easy to manipulate when fresh but hardens over time, resulting in durable and stable structures; (ii) it is water-proof; and (iii) it has antimicrobial properties (Wille and Michener 1973; Ghisalberti 1979; Roubik 1989). Thus, given its multiple uses and properties, resin is an essential component of stingless bee nests, not only in terms of structure but also for thermoregulation and defense (see below).

## 11.4 Resins for Nest and Individual Defense

Meliponines are threatened by an astonishing variety of natural enemies, including both invertebrates, such as ants, phorid flies, and spiders, and vertebrates (e.g., anteaters, chimpanzees, honey badgers, birds) (Schwarz 1948; Roubik 1989; Estienne et al. 2017; Grüter 2020). Moreover, their nests are frequently attacked by kleptoparasitic (robbing) stingless bees (e.g., *Lestrimelitta* and *Cleptotrigona*), which pilage their reserves (e.g., honey, larval food, pollen, wax) (Sakagami et al. 1993; Grüter et al. 2016). Accordingly, meliponines have developed diverse defensive strategies, often involving the use of resin, to face such threats.

Despite lacking a functional sting, meliponines are able to defend their nests by employing other defensive strategies that include biting, releasing alarm pheromones, and depositing resin, among others (Schwarz 1948; Wille 1983; Roubik 1989, 2006; Nunes et al. 2014; Shackleton et al. 2015; Grüter et al. 2016). Bees can deposit droplets of resin around the nest entrance or directly on the body of

**Fig. 11.5** Coral-like nest entrance of *Pariotrigona pendleburyi* ornamented with strings of resin beads. (From Bänziger et al. 2011)



intruders (Schwarz 1948; Wille 1983; Wittmann 1985; Roubik 1989). For example, the tear drinking stingless bee *Pariotrigona pendleburyi* builds complex nest entrances (forming a coral-like clump of tubes) ornamented with strings of resin beads (Fig. 11.5) that work as protective palisades against *Camponotus* ants (Bänziger et al. 2011). Conversely, several species of the genus *Melipona* (e.g., *M. rufiventris*, *M. seminigra merrillae*, *M. crinita*, *M. flavolineata*, *M. panamica*—formerly called *fasciata* (Camargo and Pedro 2007)), in addition to obstructing the nest entrance with their bodies, respond to the robber bee *Lestrimelitta limao* or ant raids by blocking the tube aperture and the ventilation openings with batumen balls that workers drag from within the nest to prevent the intruders from entering the nest (Portugal-Araújo 1978; Roubik 1989; Nunes et al. 2014). The arboreal species *Tetrigona apicalis* and *Lepidotrigona terminata* deposit resin droplets around their nest entrances, which have a repellent effect against the weaver ants *Oecophylla smaragdina* due to their adhesive and viscid characteristics (Duangphakdee et al. 2009). Resins used by the Australian stingless bee *Tetragonula carbonaria* have the same effect against the predatory ants *Iridomyrmex purpureus* and *Rhytidoponera metallica* (Drescher et al. 2014).

A different strategy is employed when bullet ants (*Paraponera clavata*) attempt to enter a *Partamona testacea* nest: they are dragged inside the nest and covered



with resin (Bordoni et al. 2020). *Tetragonula laeviceps* and *T. melanocephala* immobilize intruder ants (*Crematogaster difformis*, *Paratrechina longicornis*) by applying droplets of resin on them (Lehmberg et al. 2008), and *Melipona panamica* and *Scaptotrigona bipunctata* apply resin on the body of nonnestmate intruders (Inoue et al. 1999; Jungnickel et al. 2004). These uses of resin against ants also explain why some stingless bee colonies increase resin collection after an ant attack (Leonhardt and Blüthgen 2009). A peculiar strategy is displayed by *Tetragonula carbonaria* and *Austroplebeia australis* against the invading small beetle hive *Aethina tumida*. The workers attack in mass and mummify the beetle alive by covering it with a mixture of resin, wax and mud (Greco et al. 2010; Halcroft et al. 2011). Finally, besides applying resin on the body of intruders, several meliponine species can extract and incorporate resin compounds in their cuticular profiles, which protect them against pathogens, have a repellent effect against ants, and might be involved in nestmate recognition (Lehmberg et al. 2008; Leonhardt et al. 2009; see Chap. 9).

Resins might also be important against less visible threats. There is evidence that resins stored and used in nest construction have antibacterial and fungicidal activity (Miorin et al. 2003; Bankova and Popova 2007; Lehmberg et al. 2008; Sanches et al. 2017; Choudhari et al. 2012). In particular, the presence of terpenoids and phenolic compounds is effective against Gram-positive bacteria and the fungus *Candida albicans* (Velikova et al. 2000a, b; Fernandes Jr et al. 2001; dos Pereira et al. 2003; Massaro et al. 2014; Sanches et al. 2017; Popova et al. 2021a, b). Hence, resins used to build honey and brood pots as well as pillars reduce pathogen infections by preserving a sterile environment within the nest. A peculiar use of resins was described in *Ptilotrigona lurida*, a stingless bee that stores large quantities of *Clusia* spp. resins in storage pots (Camargo and Pedro 2004). *Clusia* resin, it is hypothesized, helps in the preservation of beneficial yeasts, which play an important role in the storage of pollen and its protection against bacterial contamination (Hrncir 2020).

## 11.5 Nesting Associations with Active Ant and Termite Colonies

Associations of stingless bees with termite and ant nests are well known. Wille and Michener (1973) studied 145 meliponine species and found that around 10% of them lived in termite nests, two species in ant nests, and two species in both termite and ant nests. Similar results were reported by Roubik (1983), who studied 40 species of stingless bees in Panama and found that 12% nest with termites and only one species nests with ants. Presumably, this lower frequency of myrmecophily compared to termitophily is due to the aggressiveness that ants show toward stingless bees (Sakagami et al. 1989).

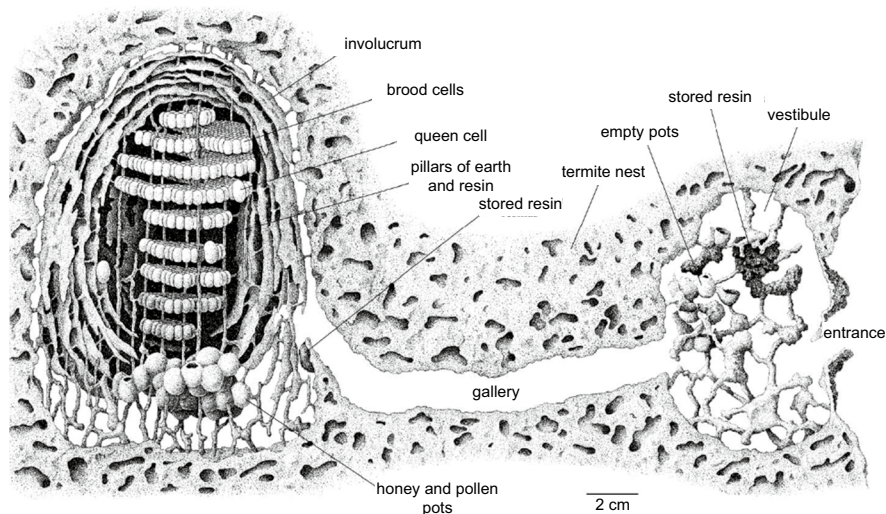
A nonexhaustive list of stingless bees nesting with termites are the genera *Trigona* (e.g., *T. pallens*, *T. ferricauda*, *T. fuscipennis*, *T. latitarsis*, *T. isopterophila*,

*T. recursa*, *T. cilipes*) (Smith 1954; Mercado 1962; Roubik 1983; Camargo and Possey 1990) and *Partamona* (e.g., *P. batesi*, *P. gregaria*, *P. pearsoni*, *P. ferreirai*, *P. chapadicola*, *P. nhambiquara*, *P. vicina*, *P. mourei*, *P. auripennis*, *P. combinata*, *P. cupira*, *P. mulata*, *P. ailyae*, *P. seridoensis*, *P. criptica*, *P. rustica*, *P. cupira*) (Camargo and Possey 1990; Nogueira-Neto 1997; Camargo and Pedro 2003). However, *P. testacea* also builds its nests associated with the bullet ant *Paraponera clavata* (Bordoni et al. 2020) or leafcutter ants of the genus *Atta* (Camargo and Pedro 2003). Another genus recorded in association with ant nests is *Paratrigona*; these bees use arboreal *Camponotus senex* nests (Camargo and Possey 1990), but can also be found associated with the ant-gardens of ponerine ants (Corbara and Dejean 1998). For its part, *Trigona cilipes* represents a particular case since its nests can be found within ant (*Azteca* sp., *Crematogaster* sp.), termite (*Nasutitermes*), or wasp (*Epipona tatuá*) nests (Camargo and Possey 1990; Rasmussen 2004).

Resins are thought to be important during colony foundation. It has been observed that myrmecophile and termitophile stingless bees initiate their nest by depositing resin balls near or on the surface of the host nest (Roubik 1989; Sakagami et al. 1989). Then, workers bring cerumen from the mother colony to build an entrance tube, and add more resin. At the same time, they excavate and extend a series of pockets in the galleries of the termite or ant nest (Roubik 1989). Since the bee nest is limited by a continuous layer of resin or batumen, the contact between bees and ants or termites is minimized and mainly occurs during the bees' nest expansion (Wille and Michener 1973; Roubik 1989; Sakagami et al. 1989). Moreover, during expansion of the nest cavity, the area of contact between bees and the host nest is sealed with resin (Roubik 1989; Sakagami et al. 1989; Rasmussen 2004). As mentioned in the previous sections, the deposition of sticky resin not only acts as a physical barrier but it also has deterrent effects against intruders, thus being effective against ant or termite attacks. Some species (e.g., *Partamona*) build a vestibular chamber adjacent to the nest entrance, filled with tangled pillars made of resin and soil. In the case of *P. vicina*, a "false nest" containing empty brood cells and empty storage pots have been observed (Fig. 11.6) (Roubik 1989; Camargo and Pedro 2003). Both the vestibule and the false nest provide space for guard bees who can act in case of an intruder attack; thus, it is presumed that the presence of these chambers could help to delay or distract attackers (Camargo and Pedro 2003).

## 11.6 Outlook

Resins are of critical importance for nest building and colony defense. Yet despite the many striking observations of resin use in stingless bees, our knowledge often remains anecdotal, and more detailed studies are needed to further elucidate the use and functions of resin in stingless bees. For instance, we still know little about the information cues and signals that are used to coordinate the different tasks involving resin collection and processing. We also do not know if workers that collect or process



**Fig. 11.6** Internal view of a *Partamona cupira* nest within an active termite nest. (From Camargo and Pedro 2003)

resins show particular physical and/or physiological traits that distinguish them from other workers, such as particular glandular secretions or a distinct sensory perception.

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