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Review article

Stingless bee nesting biology*

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Abstract – Stingless bees diverged since the Cretaceous, have 50 times more species than *Apis*, and are both distinctive and diverse. Nesting is capitulated by 30 variables but most do not define clades. Both architectural features and behavior decrease vulnerability, and large genera vary in nest habit, architecture and defense. Natural stingless bee colony density is 15 to 1500 km^{-2}. Symbionts include mycophagic mites, collembolans, leiodid beetles, mutualist coccids, molds, and ricinuleid arachnids. Mutualist bacteria and fungi preserve food and brood provisions. Nest associates include trees, termite, wasp and ant colonies. Ventilation is the means of nest environment regulation, achieved by fanning worker bees. Permanence of stingless bee nests, with annual mortality ca. 13%, implies a colony has 23 years to reproduce. Inability to freely swarm and single mating may all increase nesting specificity, competition, symbiosis and cleptobiosis in communities, while disease is rare.

Meliponini / Apidae / nest architecture / nest microclimate / evolutionary ecology

"Behind this door lives a town. They are dynamic and hardworking members of a nation whose origins go back millions of years – years of persistent and gradual evolution. If nature be treated with only steel and fire, in a short time such actions will destroy the town and its inhabitants. If, however, the heart feels kinship with the wonders that have been created, this tiny kingdom will be kept, so to better understand the earth and its residents. The well being of natural resources lies in your hands."

P. Nogueira-Neto, 1970, interpretation by present author.

"As we have stated before, honey bees are not domesticated animals. It is possible to keep bees in a hive only because we understand their biology. Beekeeping is the application of our knowledge of bee behavior."

R.A. Morse, 1994.

1. OVERVIEW

1.1. Nesting and diversity

Stingless bees have populated tropical earth for over 65 million years – longer than *Apis*, the stinging honey bees (Camargo and Pedro, 1992; Michener, 2000). Both groups make honey in perennial nests founded by a swarm of sterile workers and a queen, and colonies occasionally produce male bees. Yet stingless bees have 50 times more species and, as emphasized here, differ from *Apis* in many biologically significant ways.

Meliponines cannot migrate. Also unlike honey bees, they produce brood in the manner of solitary bees, with an egg placed on top of a food mass in a sealed cell. In general, colonies make far less honey, and therefore have less economic appeal, compared to honey bees (see Fig. A online only).

In contrast to *Apis*, meliponines generally have no sting, mate only once, do not use water to cool their nest or pure wax to build it, cannot freely swarm to reproduce (but instead must first make a new domicile), and

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* Figures A–L are available at
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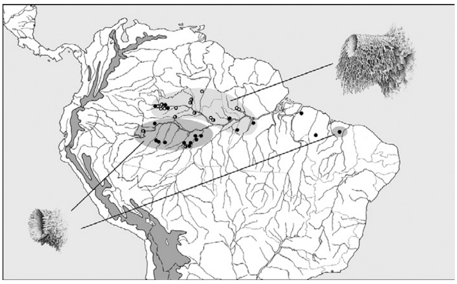

Figure 1. Distributional map of two distinctive nest entrance tubes constructed by workers of *Ptilotrigona lurida* (Camargo, from Camargo and Pedro, 2004).

the males feed at flowers, while the gravid queens cannot fly. The manifold consequences of a single mating in stingless bees, in contrast to multiple mating in *Apis*, are not explored here (see, e.g. Peters et al., 1999). Instead, a view is given of general ecological and evolutionary settings in which stingless bee colonial life takes place. The nest is the central place from which stingless bees mate, forage and pass through life stages. Nests are immobile fixtures and potentially long-lived, much like trees in forests where meliponines live. Dispersion (spatial arrangement) of colony resources and 'stress sources' have much significance, thus a primary evolutionary response of meliponines to such critical factors defines their nesting biology (Michener, 1974; Roubik, 1989; Nogueira-Neto, 1997; Camargo and Pedro, 2002a, b; Biesmeijer et al., 2005).

Published data on stingless bee nesting span over three centuries (Schwarz, 1948) and recent syntheses include Michener (1961, 1974, 2000) Wille and Michener (1973), Sakagami (1982), Wille (1983), Roubik (1989), and Nogueira-Neto (1997). Research primarily considers Neotropical stingless bees, because roughly three-fourths of all species are American (Camargo and Pedro, 1992).

1.2. Nest biology

Because nests are notable points of bee activity, often spectacular examples of animal architecture, nesting biology is a highly visible aspect of stingless bee behavior (Michener, 1974). Colonies are active every day and therefore have sustained impact among the biota (Roubik, 1989; Hansell, 1993). The individual species are recognizable from nest entrances and often their particular site – much obvious variety exists. Inside the nest, there are different shapes and arrangements of brood cells and food storage containers. Honey and pollen are stored in separate 'pots'. Stored nectar or ripened honey are in nest cavity extremes (for storage during heavy flowering periods), while pollen and some honey surround the brood area. However, robber bee genera *Lestrimelitta* and *Cleptotrigona* collect and then store some mixed honey and brood provisions (Sakagami et al., 1993). The brood cells are spherical to ovoid, while food storage containers are small to large spheres, or are egg-shaped, or even conical or cylindrical. Often pots are pressed together in odd conglomerates, as are the brood cells, ranging from individual cells on pillars, to sheets of orderly cells on combs, separated by the pillars (Fig. 3 and Figs. A, C, I online only).

Figure 2. Nest entrances of *Partamona gregaria* and *P. vicina* in a termite nest on the side of a hut (Amapá, Brazil) (Camargo, from Camargo and Pedro, 2003).

Nests made by stingless bee workers and habit (specific location) within forests (Kerr et al., 1967; Posey and Camargo, 1985; Camargo and Pedro, 2003) are foremost among traits that, along with the workers, males and queens, potentially help organize biological information with application to research, economics, and conservation of pollinators and honey sources. It is important to intensify analysis and data collection now, because in many places the original forests occupied by hundreds of stingless bee species are degraded, threatened, or gone.

1.3. Nesting evolution and variability

It is a reasonable guess that not half of all meliponine nests are known, and few have been studied adequately. Architectural innovations may occur in a taxon after its divergence from ancestors, and at the same time, unrelated species may converge due to the similarity of nesting materials or sites (see Tab. I). There is currently no clear picture as to what influence the environment versus pre-programmed bee behavior supply to nest structures. For the purpose of exploring stingless bee nesting, I generally refer to clades as genera, of which several dozen exist (see Camargo and Pedro, 1992; Michener, 2000; Camargo and Roubik, 2005). In Table I, without an exhaustive list of species, it is evident the majority of nest characteristics are shared between various genera (see Kerr et al., 1967; Camargo, 1970; Wille and Michener, 1973; Roubik, 1979, 1983, 1992; Sakagami, 1982; Dollin et al., 1997; Camargo and Pedro, 2003). Because meliponine nests incorporate a small number of apparently uniform materials, functions, and designs, there is difficulty assigning phylogenetic series, such as comb construction, to nesting attributes (see Wille, 1983; Michener, 2001). Further attempts must wait until a robust phylogeny for stingless bees is available (Camargo and Roubik, 2005; Michener, 2000; Franck et al., 2004). At present no fossil nest structures or 'ichnofossils' are known for the group, while described species and genera are still increasing. This review examines biological diversity among living stingless bees and includes my unpublished observations. The selected examples of nesting biology help to identify natural selection elements that shape nesting natural history. The nest associates, colony maintenance and defense, foraging activity, reproduction, and community ecology of stingless bees are intimately related to nesting biology of each stingless bee species, and await thorough studies.

Some large genera display considerable species-level variation in nesting habit, likely produced by adaptive radiation. Large variation occurs, for example, within the Neotropical genus *Plebeia*. The nest sites and architecture include nesting habits on tree trunks, in crevices within rocks, in holes made by other animals, hollow stems (including tree trunks) and in active termite nests. Some *Plebeia* build the regular pancake-like stack of brood cells separated by pillars and arranged in circular combs, like that made by most stingless bees, whereas the smallest species do not build combs but instead make loose chains of cells or clusters (see Fig. A online only). *Austroplebeia* build loose combs, perhaps an intermediate comb condition (Michener, 1961). Bee size appears decisive because, among tiny Meliponini, clustered cells are the architectural rule among phylogenetically diverse bees (Michener, 2001). In *Melipona*, *Plebeia*, *Plebeina*, *Nannotrigona*, *Trigona* and *Tetragona*, stacked combs or a continuous spiral of comb are sometimes built by the same colony at different times (pers. obs.). Pronounced differences may occur geographically, as documented for nest entrance tubes of Amazonian *Ptilotrigona lurida* (Camargo and Pedro, 2004; Fig. 1). Individual variation in architecture, for instance elaboration of the nest entrance (Wille, 1983; Sakagami et al., 1983; Melo, 1996) or thickness of resin enclosing the internal nest, likely relates to (1) nest age, (2) bee genetics, and/or (3) microenvironment, including predators, parasites, symbionts, rain, wind and sun. One study demonstrates that nest architecture does not diversify in pace with population divergence, detected using hypervariable microsatellite DNA in an Australian *Tetragonula* (Franck et al., 2004). Although there is currently little understanding of how micro-architectural variation may be adaptive, on some occasions, a nest construction technique can be related to constraints. For example, *Melipona* forage, and then employ in their nest construction, small pebbles and stones. Building material of this

Table I. Variables for stingless bee nesting biology, and terminology*. Because most species are undocumented in the listed traits, and variation is implicit within a genus, the list of genera is not exhaustive and an entry does not represent all species in a genus. Specific references are available from the author.

- 1, Aggressive worker defense: *Duckeola, Heterotrigona, Hypotrigona, Lophotrigona, Melipona, Oxytrigona, Paratrigona, Partamona, Plebeia, Ptilotrigona, Scaptotrigona, Tetragona, Tetragonisca, Tetragonula, Trigona*
- 2, Exposed nest: *Dactylurina, Partamona, Plebeia, Trigona, Tetragonisca*
- 3, Association with termite, ant or wasp colony: *Aparatrigona, Paratrigona, Partamona, Plebeia, Scaura, Schwarzula, Sundatrigona, Trigona*
- 4, Subterranean nest or non-arboreal, natural cavity; *Geotrigona, Lestrimelitta, Melipona, Meliponula, Mourella, Nogueirapis, Paratrigona, Pariotrigona, Partamona, Plebeia, Plebeina, Ptilotrigona, Scaptotrigona, Schwarziana, Tetragonisca, Trigona*
- 5, Irritant chemical defense: *Oxytrigona, Melipona*
- 6, Flexible entrance tube and/or nocturnal closure: *Friesella, Meliponula, Nannotrigona, Pariotrigona, Plebeia, Scaptotrigona, Scaura, Schwarziana, Trigona*
- 7, Pillars through several combs: *Partamona*
- 8, Ventilated batumen plate; *Melipona, Plebeia*
- 9, Multiple entrances; *Lepidotrigona, Plebeia, Scaptotrigona, Tetragona*
- 10, Aggregation of nests with same or other meliponine species: *Hypotrigona, Melipona, Partamona, Plebeia, Tetragonula, Scaura, Schwarzula*
- 11, Blind tubes by entrance; *Lestrimelitta, Partamona*
- 12, Drainage tube or liquid waste discharge: *Geotrigona, Meliponula, Mourella, Schwarzula, Tetragona, Trigona*
- 13, Storage pots large, either cylindrical, spherical, conical, elongate, egg-shaped, and not similar to brood cell size: *Cephalotrigona, Duckeola, Frieseomelitta, Geotrigona, Melipona, Meliponula, Tetragona, Tetragonisca*
- 14, Queen cell: size similar to workers and male, not built on edge of comb: *Melipona*
- 15, Cell construction: synchronous, *Frieseomelitta, Lepidotrigona, Lestrimelitta, Nannotrigona, Paratrigona, Plebeia*
- 16, Brood cell arrangement: not made into a horizontal comb of close cells; *Dactylurina, Friesella, Frieseomelitta, Hypotrigona, Leurotrigona, Lisotrigona, Plebeia, Scaura, Tetragonula* (Australian-Papuan), *Trigonisca*
- 17, Inquilines: leiodid or other beetles, collembolans, coccids, mites, diverse invertebrates, fungi, microbes (qualitative) *all genera*?
- 18, Trash, resin, resin ball, wax deposit (qualitative, quantitative) *all genera*
- 19, False nest or vestibule: *Partamona, Plebeia*
- 20, Imprisonment chamber: *Friesella, Frieseomelitta, Plebeia, Schwarziana, Tetragonisca*
- 21, Oviposition - Single or multiple advancing fronts; multiple fronts: *Geotrigona*, *Lestrimelitta*, *Melipona, Meliponula, Nannotrigona, Scaptotrigona, Trigona*
- 22, Local names and significance (nesting, medicinal, food, fermented beverage, incense, natural enemies, absconding or defense)
- 23, Entrance height aboveground and orientation (quantitative and qualitative)
- 24, Stored pollen consistency: with mold, or dry; *Ptilotrigona*
- 25, Honey sugar concentration, chemical properties (quantitative and qualitative)
- 26, Fecal pollen accumulation or scutellum: *Cephalotrigona, Trigona*
- 27, Sticky resin applied on outside of nest entrance, on substrate or tube: *Lepidotrigona, Scaura, Tetragona, Tetragonula, Trigonisca*
- 28, Wood fiber (paper) nest material: *Trigona*

Table I. Continued.

- 29, Cryptic nest entrances (no tube, small); *Austroplebeia, Celetrigona, Dolichotrigona, Friesella, Geotrigona, Hypotrigona, Leurotrigona, Liotrigona, Lisotrigona, Melipona, Meliponula, Mourella, Paratrigona, Plebeia, Schwarziana, Schwarzula, Trigonisca*
- 30, Hovering nest defenders; *Lestrimelitta, Tetragona, Tetragonisca*

* Terms coined for stingless bee nests are in Michener (1961), Wille and Michener (1973), Sakagami (1983) or noted below. **Cluster nest**: brood and food cells arranged in connected chains; **cerumen**: wax and plant resin mixed for pliable construction material; **involucrum**: a single or series of sheaths, made of cerumen, surrounding brood; **batumen**: thick involucrum forming a wall, or resin layer surfacing nest cavity (mud, seeds, wood, vertebrate feces may be added); **pillars**: cerumen used as anchors of nest elements; **entrance tube**: passageway connecting colony with outside; **storage pots**: containers of cerumen, sometimes nearly wax; **scutellum**: hard, thick outer nest structure (Nogueira-Neto, 1997); **imprisonment chamber**: cerumen cell attached to the nest wall, with small holes (Drumond et al., 1995); **queen cell**: generally on comb margin and larger than others, for all but *Melipona*; **advancing front**: area (s) of comb where new cells are being constructed; **exposed nest**: nest not contained in cavity; **bottleneck**: small tube leading into brood area (Camargo and Pedro, 2003); **false nest, vestibule**: area near entrance containing empty pots or cells (Camargo and Pedro, 2003); **resin deposit**: small mound of resin on nest floor or wall; **wax deposit**: similar to resin deposit; **entrance tubercles**: hollow finger-like projections; **paper nest**: outer nest covering made mostly of wood pulp (Roubik, 1989); **advancing front**: open brood cells, which can be made either **synchronously** (all at the same stage of completion) or **continuously** (at all stages at any time).

mass could not even be lifted by most stingless bees.

One highly distinctive trait, vertically oriented comb with horizontal cells, has clearly arisen twice. That trait is recorded in one Neotropical and one Afrotropical genus, *Scaura* (Nogueira-Neto, 1997) and *Dactylurina* (Darchen, 1972) respectively, and in only one of five species in the former (Tab. I).

2. PLATFORMS FOR DEFENSE AND FORAGING

2.1. Nest defenses

The site and architecture of stingless bee colonial nests represent compromises between nesting material, nest location and a combative versus cryptic colony profile. Honey hunters, both primate and presumably other vertebrates, use nest entrances, with noises and the sight of bees in flight or ventilating the nest, to locate stingless bee colonies. In one study of over 200 nests in Uganda, nest predators (primarily tool-using chimpanzees and humans) most affected colonies in trees at under seven meters height (Kajobe and Roubik, 2006). However, common stingless bees with large colonies, and resources for predators to consume, also nest in the ground, approximately from 20 to 200 cm depth (pers. obs., see Tab. I).

Only when nests are opened are the defensive behavior, such as attack or immediate retreat, and the internal nest architecture revealed. However, defensive responses to individual small predators, such as insects that catch bees by nests, are rarely studied. In a study of Panamanian colonies including 40 species, half showed no defensive biting behavior toward the observer (Roubik, 1983). Bees were timid when approached, and retreated within the entrance. Stingless bee keepers might tend to select gentler species, but this is not the case, with half of those well-known in Brazil able to actively defend nests from large vertebrates (see Nogueira-Neto, 1970). Many species are tremendously aggressive and attack while biting, applying sticky resin carried in the mandibles or on hind legs. Among 'fire bees', *Oxytrigona*, and a few others (reportedly *Melipona rufiventris* in Bolivia, Stierlin, pers. comm.), caustic secretions, containing formic acid in the former, are applied (Michener, 2000). Bees of this nature emit disagreeable odors from mandibular gland secretions and seem to take special care to fly into the hair, ears, eyes or mouth, and emit distressing sounds. Accordingly, most nests that are exposed and easily attacked by predators have aggressively defensive workers, regardless of bee size or phylogeny (Sect. 2.3). An exception is the genus *Dactylurina* in Africa (Eardley, 2004), which have exposed nests but lack aggressive defensive behavior (Darchen, 1972). Moreover, colonies that appear well protected, settled within several cm of living tree trunk and having a small nest entrance, can be either aggressive or timid (Sects. 2.3, 2.6).

Defending bees normally come from the entrance area and nests have suitable architectural features to allow their aggregated presence there (Tab. I; Figs. 1, 2 and Figs. B–F, I online only). Defensive strategies include alarm chemicals of mandibular gland origin, released in the air within and outside the nest (Smith and Roubik, 1983; summary in Roubik, 1989; Wittmann et al., 1990). Hovering defenders then exit in force, face the nest entrance, and engage in aerial fights with non-nestmates, or directly attack larger animals, which retreat with a cloud of defending bees surrounding the head. Very few species, for example *Tetragonisca angustula* and *Tetragona clavipes*, regularly maintain hovering defenders outside the nest. Hovering 'guard' bees may defend against the robbing bee, *Lestrimelitta* (Wittmann et al., 1990), or against raiding individuals from other meliponine colonies (Sakagami et al., 1993; Sect. 5.2).

2.2. Defense materials

The primary activity of non-foraging bees near their nest entrances is prevention of entry by small insects, including parasites, and for the deposit of fresh resin on external entrance tubes, which may deter ants (see Fig. L online only). The chemistry and choice of nest resins useful as repellants of natural enemies has not been studied, although the antibacterial properties of resins are well known (Lokvam and Braddock, 1999; Langenheim, 2003). *Symphonia globulifera* (Clusiaceae) provides a steady resin source that is mined daily and defended by several nest mates of *Trigona fulviventris* (pers. obs.). Resinous material deposited by female *Centris* on terminal nest cells are used by individuals or small groups of aggressive *Trigona fuscipennis* and *T. muzoensis* in Panama (pers. obs.). Resin sources are generally wounded trees, and they often have several species visit them, including bee predators, some of which are stingless bee mimics (Roubik, 1989).

Nesting cavities with extensive sprays of resin droplets, for several cm from an entrance, can be found on stems with nesting colonies of African *Meliponula ferruginea* (see Fig. I online only) Neotropical *Trigonisca* and Asian *Geniotrigona thoracica*, among others. The use of resin to immobilize large beetles within the nest has been well documented (Nogueira-Neto, 1997). Resin is usually placed on predators' hair, and it is applied to objects near the nest entrance.

In *Melipona panamica* and other *Melipona*, hardened balls of resin are loosely cemented by the entrance; when needed, the spheres *may* be rolled into place, cemented together with resin and thus close the entrance to invaders (pers. obs.); spheres tend to accumulate in older nests at their bases (see Fig. B online only). Honey has been recorded as a defense material employed by tiny *Hypotrigona braunsi* in Africa (Portugal-Araújo, 1958; Michener, 1959).

Few stingless bees make a defensive wall of enough thickness to permit use of nest cavities that have large openings; these are *Melipona*, *Cephalotrigona* and *Meliponula bocandei* (Portugal-Araújo, 1955; Roubik, 1983). As mentioned above, *Melipona* use small stones. Colony batumen, separating the inner nest from the outer environment, may be built to a thickness of 10 cm with the stone, mud and resin mix made by *Melipona* (see Fig. B online only). Workers of *Melipona* are, apparently, unique in the behavior of surveying the outside of both nest and hive for sharp edges, openings or other irregularities, then depositing material on them (see Fig. D online only). Ramirez (1996, pers. comm.) noted that worker *Trigona corvina* prunes twigs and removes leaves in front of the nest entrance.

2.3. Protection of the outer nest

There are completely or partly exposed nests built on stems or hard substrates by aggressive *Trigona*, *Tetragonula*, *Tetragonisca*, *Partamona*, *Paratrigona* and *Plebeia*. Many unaggressive species, including those within most the abovementioned genera, nest in living trees, but those with exposed nests have an outer nest shell that is delicate, and workers immediately flood from the exterior of a broken nest envelope, then bite. Biting behavior in defense against vertebrates has no direct relation to bee size. *Tetragonula fuscobalteata* is among the most aggressive and also the smallest native stingless bees in SE Asia. Aggressive colonies can be aggregated in a single palm branch (pers. obs., Brunei), whereas stem-nesting colonies, ostensibly the same species, are unaggressive (Sakagami et al., 1983, Peninsular Malaysia). Tiny *Plebeia minima* builds a nest on spiny palms (*Bactris* and *Astrocaryum*), sometimes in small aggregations, and the workers have strong biting responses to molestation (Roubik, 1983). Similarly aggressive *Tetragonisca weyrauchi* builds exposed nests (Rasmussen, pers. comm.; Cortopassi-Laurino and Nogueira-Neto, 2003).

A noteworthy meliponine defensive structure is the ‘scutellum nest’ of Neotropical *Trigona*. This hard and thick barrier is made by exposed-nesting *Trigona* (Nogueira-Neto, 1962), by hypogeous *T. fulviventris* (Roubik, 1983), and is an ample protective shield (Wille, 1983). Nogueira-Neto (1962) noted the scutellum is made up largely of bee feces. After microscopic analysis, Roubik and Moreno (pers. obs.) find the scutellum of *Trigona corvina,* up to half a meter thick, is composed of pollen exines – feces of pollen consumed by bees. Often surrounded by a few thin batumen covers, layers outside of the scutellum are easily broken by predator attack, thus function to permit release of many defending bees from throughout the nest surface. In similar nests, *T. spinipes* opens holes in the outer nest shell in response to temperature and ventilation needs (Sakagami and Zucchi, 1972, in Sakagami, 1982), thus the thin shell may have more than one function.

2.4. Nest entrance platforms

The simplest stingless bee nest entrance protrudes slightly from the base of the entrance hole. Nest entrances are not only related to defense and foraging (Biesmeijer et al., 2005), but to physio-chemical regulation, as discussed below. A small or unornamented nest entrance is cryptic (see Fig. F online only), and is usually the only passage to a relatively small number of potentially defensive adult bees. The narrow tube can be closed with resin or cerumen, or coated outside with droplets of fresh resin where invaders like ants may be halted (Wittmann, 1989; Camargo, 1984, see Fig. I online only). Larger species, for example *Melipona, Cephalotrigona* and *Scaptotrigona* (see Fig. B online only) also build long and/or wide *internal* nest entrance tubes, where foragers, ventilating bees or defenders are positioned. In addition, the inside alcove of the nest entrance of *Partamona* (Camargo and Pedro, 2003), often holds decoys of empty storage pots or brood (Fig. 2), which may confuse and discourage predators who probe, such as long-tongued anteaters, *Tamandua*. A few *Partamona*, such as *P. pearsoni* and *P. peckolti* also have the brood chamber blocked to all entry, save through a secondary entry ‘bottleneck’ (Camargo and Pedro, 2003; Fig. C online only).

The largest nest entrances are those made by certain *Trigona*, *Tetragona*, and *Scaptotrigona*, in tropical America (see Fig. B online only) and *Homotrigona* and *Geniotrigona* in Asia. Some are aggressive species, and they may be mimicked by other, inoffensive bees in the same forest. For instance, *Trigona fuscipennis* and *T. necrophaga* have similar large-scooped nest entrance structures, but the latter displays no aggressive nest defense behavior, and a parallel relationship may exist between *Trigona crassipes* and *T. fulviventris*, which build long, wide resin entrance tubes (see Roubik, 1979, 1983; Camargo and Roubik, 1991).

African and Australian meliponine bees have no such large or conspicuous entrances. In contrast, the largest bees in SE Asia, *Geniotrogona thoracica* and *Homotrigona fimbriata* have enormous, projecting nest entrances, so large (a few kg and up to 50 cm in length) that their weight makes them periodically fall from trees (Roubik, 1993 and pers. obs.; Roubik et al., 2005). Those large bees have no accessory galleries or lamellate passageways at the entrance, and no aggressive nest defense. The building of a very long but slender nest entrance tube by Neotropical *T. cilipes*, Asian *T. collina*, and related species, derives from placing fresh resin on the tube (pers. obs.; see Fig. I online only). In contrast, aggressive (toward humans) Asian *Heterotrigona canifrons* and *H. itama* (Sakagami et al., 1983) have relatively small, simple entrance tubes.

2.5. Entrance refinements

A defense employed by diverse meliponines is closing the external nest entrance at night, usually accomplished with a 'curtain' of a loosely knit (spaces are visible between the mandible-carried bits of resin and cerumen) sheet that covers the entrance. This certainly implies that resin or mere barriers are effective against small parasites (Sect. 4.6) or ants.

Although large nest entrances are staging areas both for foraging and defense, an elaborate entrance or large exit hole are not necessary for effective defense against small natural enemies – largely within the nest – or for aggressive attacks outside, on marauding vertebrates. Given appropriate alarm pheromones, bees stream outside the nest, as in *Melipona panamica* (pers. obs.), and the absolute size of a nest entrance need not be associated with intensive forager traffic (Roubik et al., 1986). Recently, however, an analysis of foraging activity and external nest entrance size revealed a positive correlation (Biesmeijer et al., pers. comm.). Nest entrances of most *Partamona* are made like a baseball glove (Camargo and Pedro, 2003; Fig. 2), allowing either large influx of incoming foragers to be funneled in, or the exit of defending bees, but there is only a relatively small hole at the base of the 'funnel'. The entrance of Mexican *Lestrimelitta niitkib* designs its entrance for heavy traffic (see Fig. F online only). The single largest stingless bee nest entrance is of aggressive *Trigona silvestriana* (syn. *truculenta*), in the Peruvian Amazon (see Fig. C online only). The only other meliponine with such a structure is *Geniotrogona thoracica* (pers. obs.) but that of *T. silvestriana* is a hard resin tube, nearly a meter in length and 10 cm in diameter, with hard resin lamina along its inside axis, thus a

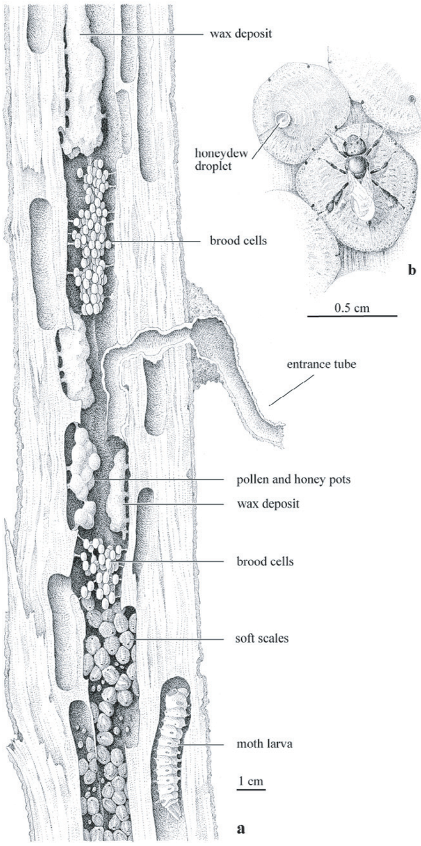

Figure 3. The nest gallery of *Schwarzula coccidophila* and its symbiont coccid (Hemiptera) *Cryptosternum*, scale insects which produce wax used by the bees for nesting (Camargo and Pedro, 2002b, Camargo (Copyrighted 2002 by the Association for Tropical Biology, P.O. Box 1897, Lawrence, KS 66044-8897. Reprinted by permission)).

large surface area on which many bees assemble (see Fig. E online only).

Lestrimelitta (see Fig. F online only) and aggressive *Partamona* make hollow tubes or 'tubercles' around the exterior nest entrance. The former are unaggressive toward vertebrate predators at the nest. However, robber bees routinely engage in battles with rival colonies (Sakagami et al., 1993), and the fights may be shortened by decisive battle. Blind tunnels seem purely defensive in both contexts. Their adaptive significance is to increase the available surface area for defending bees, in the same manner as a large-bore entrance, lamellate plates in nest entrance tubes for exiting foragers, ventilators and defenders, or multiple platforms and exit holes on the tube, e.g. those of *Tetragona clavipes* (Roubik, 1979). Breaking the tubercles of *Partamona* releases a stream of defending bees. Asian *Tetragonula pagdeniformis* (see Fig. E online only) possess rootlet-like resin structures on the external entrance, much like those of Neotropical *Tetragona dorsalis* (Roubik, 1979), whose function is unknown. The many hanging rootlet-like structures surrounding the nest entrances of *T. corvina*, *T. spinipes*, *T. amazonensis* and other aggressive, Neotropical *Trigona*, and *Ptilotrigona* (Camargo and Pedro, 2004; Fig. 1) may also provide positions for defenders. Although the outer nest layers and blind tubes have been discussed as sites for trash deposit (Rau, in Nogueira-Neto, 1948) and insulation (Drumond et al., 1995), their primary known function relates to defense.

2.6. Group protection

Aggregations of colonies occur on natural and artificial substrates, including building or hut walls and roofs (Fig. 2). Natural substrates are cliffsides or dense branches. The most common animal-based substrates are termite nests – exposed, underground, or within a tree cavity. Camargo and Pedro (2003) list *Syntermes, Nasutitermes, Amitermes, Constrictotermes,* and *Terme*s as Neotropical hosts, and also the large mound of nesting debris surrounding a colony of attine ants. Such aggregations allow pooled defense against large predators. Direct molestation, rather than the release of alarm pheromone dispersed in the air, evokes multicolony attack in *Partamona peckolti* (Roubik, 1983). Numerous species of this genus are defensive (see Camargo and Pedro, 2003). Group defense occurs among small meliponines such as *Hypotrigona* (Kajobe, pers. comm.; Michener, 1959) and *Tetragonisca weyrauchi*, but not Asian *Tetragonula* or *Heterotrigona* (Starr and Sakagami, 1987) or *Scaura tenuis* (see Kerr et al., 1967), which form aggregations.

3. NEST CONDITIONS, MATERIALS, AND MAINTENANCE

3.1. Internal nest environment

Within the closed nests of stingless bees, conditions tend to be relatively stable, but subject to daily cycles. Ventilation has been studied by Nogueira-Neto (1948) and more recently by Moritz and Crewe (1988, see Fig. H online only). Nests 'breathe' in the sense that tidal gas exchange occurs frequently, although the entrance tube is the only connection to outside. Circulation is accomplished by workers that fan their wings while facing outward toward the entrance. Variation in the number of nest entrances (some *Plebeia* and other genera have two or three separate, yet very proximate, entrance holes) were shown to allow air to exit from one hole and enter in another, by the use of smoke experiments (Nogueira-Neto, 1948). However, air is drawn into the nest and circulates, depending on physical properties of the nest, the entire living colony, and the cavity, to exit at intervals. Such 'tidal volumes' could be calculated for two African stingless bees, one nesting in the ground and one in a tree cavity. Worker bee ventilation (wing fanning activity) exchanged the entire nest air in 1–7 hours (Moritz and Crewe, 1988).

Both carbon dioxide narcosis and critically high temperatures (> 35.5 °C) were problems for the African stingless bees studied by Moritz and Crewe (1988). In the extreme ambient temperatures near the ground nest (see Fig. H online only), tidal inflow could raise the nest temperature to a fatal level, thus ventilation was diminished at the highest ambient temperatures, maintaining the cooler air within the nest cavity. Oxygen level thereby decreased, and CO_2 increased during the day, thus CO_2 was reduced by bee fanning only at night. Although the change in nest temperature in the shaded tree cavity was minimal, both the tree cavity and ground nest displayed a temperature gradient. Lethal nest temperatures were recorded at 46 °C for *Tetragonula carbonaria* (Amano, 2005) and 41 °C for *Scaptotrigona postica* (Macieiera and Proni, 2004).

3.2. Brood and involucrum areas

The brood area forms the thermal core of a stingless bee nest, where heat may be kept in (or out) by concentric involucra. It has long been speculated that the involucrum layers surrounding the brood permit heat to be retained there (reviews by Nogueira-Neto, 1948; Kerr et al., 1967). Circumstantial evidence indicates that *Melipona* may build more involucrum (see Fig. G online only) in cooler climates than in equatorial forests (Engels et al., 1995); however, a colony that is starved will build less involucrum (Kolmes and Sommeijer, 1992). Work with hives of *Melipona* (Roubik and Peralta, 1983) showed that two species, each with an involucrum, actively and/or passively (via nest architecture) controlled the nest temperature within the brood area. Recent study with *Tetragonisca weyrauchi* (Cortopassi-Laurino and Nogueira-Neto, 2003) showed similar dynamics, with the addition of an architectural innovation, a ‘respiracle’ or facultative opening on top of the nest cavity. Because brood remained over 31 °C, well above ambient temperature in the shade, heat from the bodies of the bees, especially adults between the brood combs, is likely responsible for heating the brood area. ‘Social thermoregulation’ may or may not be required, in general, because nest temperatures are not precisely controlled and bees are seemingly more tolerant to brief chilling, at least in some genera (Engels et al., 1995; Drumond et al., 1995).

The involucrum is also a barrier, with drier cerumen leaves or sheaths outside of the brood area (usually 2 to 5 in number) and a labyrinth of openings and passageways surrounding the brood (see Fig. K online only). The involucral sheaths may be significant, therefore, in preventing direct access to the brood, and the open brood cells in particular, by parasites such as phorid (*Pseudohypocera*), stratiomyid (*Hermetia illucens*), and other flies, ants, or robber stingless bees (*Lestrimelitta* and *Cleptotrigona*), and possibly the lesser wax moth *Achroia grisella* (Cepeda-Aponte et al., 2002).

3.3. Diverse behavior, materials and hygiene

Fanning during night or day should be influenced by colony honey production (Nogueira-Neto, 1948). The fact that stingless bees use nectars that average about 65% water, then convert this to honey of 30% water (Roubik, 1989; Roubik et al., 1995) means that moisture must be removed from the nest cavity. The large batumen plates having many air channels, made by *Melipona* and some *Plebeia* (Nogueira-Neto, 1948; Roubik, 1979, pers. obs.) seem ideal for the purpose of water loss. However, as mentioned above, CO_2 loss may also be significant, and other nest entrance features involving surface area and openings determine available fanning positions for bees. Water is often carried by worker bees (imbibed) and dumped from the nest entrance area, sometimes leaving wet marks near the nesting cavities (see Fig. H online only). Apart from this, latrines are maintained within nests, where several symbionts live (Sect. 4.5).

Drainage outlets are maintained in the nests of subterranean stingless bees, such as *Meliponula* and *Plebeina*, and in tree-nesting species including *Trigona* and *Tetragona,* plus exclusively ground-nesting *Geotrigona* (Portugal-Araújo, 1955; Sakagami, 1982; Camargo and Wittmann, 1989; Camargo and Roubik, 1991; summary in Camargo and Moure, 1996). The nesting cavities are not constructed by the bees, are often left by failed *Atta* colonies in the Neotropics or termites in Africa, and are modified so that water can be ejected. Nesting by some subterranean colonies takes place just above a soil horizon of very well drained material (see Fig. F online only) thus nest drainage from rain or water from ripening of honey should pose no special problem (Camargo and Wittmann, 1989).

The insulation provided by wood and resin, earth, stone, or other nest substrates, make it unlikely that colonies overheat, provided nests are not in full sunlight and not too many bees engage in fanning during extremely high ambient temperatures. As demonstrated by Moritz and Crewe (1988) tidal air flow may cause hot external air to enter the nest. Compared to resin, wax is much more rigid and four times stronger, especially at temperatures higher than 35 °C (Hepburn and Kurstjens, 1984), yet stingless bee cerumen has a higher melting temperature (Buchwald et al., 2005).

No comparative study has been made on relative amounts of resin and wax used in cerumen of different stingless bees. Small *Hypotrigona*, *Trigonisca, Schwarzula* and *Plebeia* use very little resin, using almost pure wax (Sakagami, 1982; Blomquist et al., 1985; Drumond et al., 1995; Camargo and Pedro, 2002a). Such an adaptive response by small stingless bees nesting in slender stems and exposed to high temperatures would be expected from the thermal conditions, as would a loose nest element architecture and large cavities, which allow adult movement as heat sources, or migration. Daily dynamics of air temperature have not been measured among the outer nest batumen layers in the large, exposed nests, although temperature measurements (Zucchi and Sakagami, 1972; Wille and Orozco, 1975; Roubik and Peralta, 1983) and direct observation of incoming foragers reveal no use of water droplets to cool nests (Moritz and Crewe, 1988; Engels et al., 1995; Nogueira-Neto, 1997). When water is collected by workers, it is likely to be used for honey dilution.

Nest repairs incorporate available nesting material. Workers do essentially all the work, even though males occasionally perform superficially similar (i.e. irregular) maintenance activity (Velthuis et al., 2005). Workers make wax that is secreted from dorsal glands, but some queens or males also make a small quantity; the wax is first placed on a wax deposit in the nest (Cruz-Landim, 1967; Michener, 1974; Sakagami, 1982; Koedam et al., 2002). Different stingless bee waxes have different chemical properties, and are much simpler than wax of *Apis* (Blomquist et al., 1985). Cerumen, the product of plant resin mixed with wax and employed exclusively by meliponines, remains soft for an extended time and is more pliable than beeswax – that of *Apis mellifera* (Hepburn and Kurstjens, 1984). In addition to being used for constructing nest forms, cerumen may be taken to make an emergency repair of natural enemy damage.

Cerumen is normally made freshly to construct brood cells, involucrum, nest entrance tubes, or storage pots. The wax is taken from a pure wax deposit and combined with resin taken from a pure resin deposit (see Fig. K online only). These may be in several positions near the nest entrance and brood cells; workers mix the materials with their mandibles (Michener, 1974; Sakagami, 1982). In response to drastic nest alteration, such as opening of the nest, bees respond by seeking and collecting more resin and, in genera such as *Plebeia*, *Melipona*, *Cephalotrigona*, and *Partamona*, mud is deposited directly on the edges of the opening (always interspersed with resin), which is then gradually closed, by working toward the middle. I briefly experimented with a nest of *Trigona nigerrima*, which is one of the three *Trigona* that, like certain wasps, construct paper nests from chewed wood pulp (Roubik, 1989). A 5 cm square of the nest surface was removed during the evening. The following morning the nest had been repaired, without incoming material.

When a nest is severely damaged, colonies cannot fly with their queen to a new nesting site, but a queen deprived of food did fly to an empty hive box in *T. laeviceps* in Sumatra (Inoue et al., 1984). Abandoned intact brood comb with males of *Melipona fulva* present was an indication of absconding (Roubik, 1979). *Melipona* and presumably other stingless bees aggregate on nearby tree trunks when their nest is destroyed. Whether they can survive to establish a new nest, using a flying virgin queen, or merge with another colony after such occurrences, is unknown. However, a mixed colony nesting association has been documented for *Melipona panamica* and *M. fuliginosa* (Roubik, 1981) and has been encountered in the field a second time since that report. The largest stingless bee, the latter species, makes a nest that is occupied secondarily by the smaller species, whose workers feed it nectar outside the nest entrance when returning from the field. Ultimately, as in parasitic *Bombus* (Goulson, 2003) the nest may be usurped by the newcomer species. *Melipona* are keenly interested in returning to a damaged nest and collect resin from resin deposits, and also cerumen and honey, as do many stingless bee genera.

Bees eject water, as explained above, but are far more regularly seen ejecting a bolus of trash, carried in the mandibles. This activity may occur daylong, or primarily in the afternoon. A few genera, like *Lestrimelitta*, *Hypotrigona* and *Trigonisca* (pers. obs.) drop the bolus from the nest entrance, while most, like *Melipona,* fly to drop trash meters from the nest (Kerr and Kerr, 1999). Trash balls are mainly meconia (larva defecations) on cell bases. Adult defecations in the nest are gathered at small latrines; most are consumed by mutualist organisms (Sect. 4.6). The cerumen coat is immediately removed from a newly spun pupal cocoon (Michener, 1974).

4. NESTING ASSOCIATES

4.1. Biological nest requirements

Stingless bees carefully select where to build nests, often within a living woody plant. There are thus always associated organisms, which occur there or in the immediate environment. In addition, no thorough review of organisms associated with a stingless bee nest is possible, because taxonomic names are often lacking and studies are far from complete in natural habitats (Kistner, 1982; Roubik, 1989; Eickwort, 1990; Nogueira-Neto, 1997). An exception is in the extraordinary series of nesting associations reported in Brazil by Camargo and Pedro (see 2002, 2003, 2004).

4.2. Collaborators, parasites or commensals?

Living within stingless bee nests, the mites, collembolans, leiodid beetles, mutualistic fungi or bacteria seem normal, and some nest associates seem to have become semi-domesticated. Considering the nest site, nesting in an active termite or ant nest is obligate, yet rare, among stingless bees, although the use of cavities left by termite or ant colonies is also known (Tab. I). Nest construction in abandoned bird nests is documented for *Partamona musarum* and *P. helleri* (Camargo and Pedro, 2003).

Although no exchange of material occurs, the 'host' ant or termite colonies often do not obtain or share protection from stingless bee colonies. *Aparatrigona*, *Scaura*, *Nannotrigona mellaria* and some *Trigona* (*mazucatoi, cilipes*), *Paratrigona pannosa* (Dejean and Roubik, pers. obs.) and *Sundatrigona moorei* (Sakagami et al., 1989) are parasites in terms of lodging and defense. The bees have no aggressive defense but use the nests of pugnacious *Nasutitermes, Dolichoderus*, *Azteca* (Kerr et al., 1967), *Epipona* (Rasmussen, 2004), *Pachycondyla goeldii* (Dejean and Roubik, pers. obs.), and *Crematogaster,* respectively (further references in Roubik, 1989). In contrast, *Partamona* and most *Trigona* are aggressive and associate with a variety of hosts. Even birds may derive benefits from aggressive *Trigona* colonies near their nests (Smith, 1968). Indeed, Stierlin and I observed *Sarcoramphus papa* in lowland northern Bolivia, nesting in the crown of a tree, near a nest of highly aggressive *Trigona amazonensis*. In each case, parasitic flies are *possibly* kept out of the bird nests by aggressive bees.

4.3. Microbes

Bacillus of several species, most the same as those found in nests of honey bees, *Apis mellifera*, occur in the stored pollen or brood provisions. These include *Bacillis megaterium*, *B. circulans* and *B. alvei,* which produce enzymes that may facilitate storage and/or digestion, plus secrete antibiotics and fatty acids (Gilliam et al., 1990). The yeasts *Candida* (Camargo and Pedro, 2004) and *Starmerella meliponinorum* also are mutualists in bee nests (Teixeira et al., 2003). Camargo and Pedro found yeast covering stored pollen of *Ptilotrigona lurida*, which dehydrated and preserved the pollen, also potentially supplying carbohydrates to bees, and likely making the nest less attractive to the main natural enemies, phorid flies.

4.4. Non-floral plant mutualisms?

Many stingless bee associates are trees, which of course provide both food and nest sites. At present, we do not know whether there are plants which attract stingless bees for nesting due to pollination benefits. The gathering of floral resins for nest material has been used at least by two tropical plant genera as a basis for pollinator attraction (Armbruster, 1984). However, whereas studies in relatively species-poor dry tropical forests show that only a few tree species are used by the stingless bee fauna (Moritz and Crewe, 1988; Camargo and Pedro, 2002a; Antonini and Martins, 2004; Martins et al., 2004), most studies document use of many families and genera (Hubbell and Johnson, 1977; Johnson and Hubbell, l986; Oliveira et al., 1995; Eltz et al., 2002, 2003; Kajobe and Roubik, unpublished data), with apparent exception in a hyperdiverse Asian forest (Samehima et al., 2004). Among strangler figs and their host trees, a disproportionate abundance of stingless bee nests occur (Cameron et al., 2004; Roubik and Harrison, pers. obs.). Potential pollination benefit to the figs is not possible, and for the other trees would be fortuitous.

Some resins used by meliponines carry small seeds from fruit of *Coussapoa asperifolia* (Cecropiaceae, see Garcia et al., 1992), such as those embedded in the mud and resin batumen block of *Melipona*. Such seeds were previously confused (Roubik, 1989) with *Vismia* (Clusiaceae). *Trigona carbonaria* collects resin with the seeds of *Eucalyptus torelliana* (Wallace and Trueman, 1995). The importance of seeds in nest construction is unclear, but the seeds of both plants (*Coussapoa* is a hemiepiphyte) germinate on the outside of the bee nests (pers. obs.).

4.5. Mutualist inquilines

Schwarzula coccidophila (Camargo and Pedro, 2002a, b) and *Schwarzula timida* (Roubik, Stierlin, Harrison, Kondo, pers. obs.) receive wax bugs *Cryptostigma* (Coccidae: Hemiptera) as coinhabitants of their nests, which presumably exist only because they are protected by the stingless bees, and provide valuable wax and sugar in return (see Fig. 3). Such coccids, which feed on plant sap, also live with ants, to which they give sugar secretions in exchange for protection. Intricacies of cohabitation may ultimately involve cavity utilization by different organisms, which evolve complex interdependencies.

The leiodid beetles, or scotocryptines *Scotocryptus*, *Scotocryptodes*, *Synaristus*, *Parabystus* (Roubik and Wheeler, 1982; Peck, 2003; Fig. K online only) live in nests of Neotropical genera, primarily *Melipona,* and also *Cephalotrigona* and *Partamona*. Beetle adults are blind and flightless; the males and females, often a few dozen, live among the pollen fecal debris and consume that resource (Peruquetti and Dias Bezerra, 2003), fungi or slime molds (which also consume fungi) in wet parts of the nest (Roubik and Wheeler, 1982). Dispersal of beetles occurs on hindlegs of *Melipona* (Nogueira-Neto, 1949). Adult beetles have a special mandibular notch that secures their 'ride' holding on the worker bee corbicular hairs, and transfer between nests occurs at muddy flats where bees collect nesting material (Roubik and Wheeler, 1982).

Documented residents in stingless bee nests also include ricinuleids, very slow-moving arachnids, *Cryptocellus gamboa* (Platnick, pers. comm.; see Platnick and Shadab, 1981) in the hypogeous nests of *Trigona fulviventris* in Panamanian rain forest (pers. obs.). Pseudoscorpions, *Dasychernes*, were abundant in the nest of another *Melipona* in Colombia (Salt, in Kistner, 1982). Cyphoderid collembolans *Paracyphoderus*, *Cyphorderus* and *Pseudocyphoderus* are common in nests of *Melipona* and *Partamona*. These fungus feeders, like leiodid beetles, have morphology suggesting persistent associations with the bees (Kistner, 1982). They are tough and can hide or tuck away their appendages.

Many mite genera occur in stingless bee nests and eat fungi – *Neotydeolus*, *Macrocheles*, *Tyrophagus, Trigonholaspis* and *Hemileius*, while others, apparently less numerous, feed on pollen, such as *Pyemotes*, *Lasioseius*, *Glycyphagus*, *Neocypholaelaps* and *Tyroglyphus* (Delfinado-Baket et al., 1984; Baker and Delfinado-Baker, 1985; summaries in Eickwort, 1990; Nogueira-Neto, 1997). The predaceous laelapid mite *Neohypoaspis ampliseta* feeds on astigmatid mites in stingless bee nests (Delfinado-Baker et al., 1983). Michiliid flies (Melo, 1996) also consume fecal debris in nests of at least one *Melipona.*

4.6. True parasites and predators

Considering Diptera, the internal and nest parasites of meliponines include three genera of Phoridae, *Pseudohypocera*, and internal adult bee parasites, *Apocephalus* and *Melaloncha* (Brown, 1997). Those flies, the first in particular among the worst enemies of the Neotropical fauna, are completely absent (as bee natural enemies) in the Old World. They mate hovering in copula near the nest entrance, then invade the nest and lay their eggs in all crevices or small spaces (Sect. 3.2). Evidently parasitic mites can infest larvae of *Melipona, Meliponula* and *Trigona,* and include *Meliponaspis, Hypoaspis* and *Trigonholaspis* (review by Kistner, 1982).

The largest predators of stingless bee nests are the mustelids, bears and primates, with anteaters *Tamandua*, *Myrmecophaga*, and armidillos (and other, less fearsome omnivores, such as procyonids or coatimundis *Nasua*, civets Civerridae, and opossums Didelphidae), all of which are opportunistic predators of stingless bee colonies. Mustelids are major colony enemies in the Neotropics (*Eira barbara*) and *Conepatus* hog-nosed skunks, while in savanna-dominated Africa, honey badgers (*Mellivora capensis*) and their mutualist birds, *Indicator*, are deft colony predators. Bears – *Tremarctos*, *Helarctos*, *Ursus*, are significant predators in Andean South America and SE Asia (Roubik, 1989). African rain forests have primates as principal bee colony predators - chimps, gorillas and baboons (*Pan, Gorilla, Langur*) but the honey badger is almost absent in dense forest. Australia lacks any significant stingless bee nest predator, as do Madagascar and some large islands with stingless bees, such as Taiwan and Philippines.

5. COLONIAL COMMUNITIES

5.1. Reproduction and nesting

The relative numbers and positions of colonies within an area have perforce shaped the evolution of stingless bees. Virgin queens accompany swarms of workers to new nest sites, and males wait there in anticipation (reviews in Nogueira-Neto, 1997; Velthuis et al., 2005) – clearly indicating the queen odors are dispersed from the nest. Afterwards, the new queen flies out for a single mating, pursued by hundreds of males (Peters et al., 1999; Palmer et al., 2002). The queen may be killed, or indeed, several queens are killed by predators (Michener, 1961; Paxton et al., 2003) on such mating attempts. Therefore, reproductive biology of stingless bees includes the connection for food, and potentially for new virgin queens, between the mother and daughter colony. The relationship has been documented to last up to six months (Wille and Orozco, 1975; Sakagami et al., 1983; Drumond et al., 1995).

The mean 'nearest neighbor' distance between conspecific colonies nesting in nature may be on the order of 50 to a few hundred meters (Hubbell and Johnson, 1977; Breed et al., 1999; Samejima et al., 2004). Cameron et al. (2004) estimated that 132 colonies with males participated in a mating, by analysis of microsatellite DNA markers. At a nest density of 3 ha^{-1} (the species studied, *T. collina*, has aggregated nests) colony reproductive ecology potentially included all colonies in 50 ha.

5.2. The cost of stability

Bee diseases are more frequent and well-known in honey bees than in stingless bees (Nogueira-Neto, 1997; Morse, 1994), which implies that meliponines, in contrast to tropical *Apis* (Akratanakul, 1986), do not experience strong selection to regularly change nesting sites, in order to shed their parasite load. Further, a sustained connection between mother and daughter colony provides evolutionary pathways for parasitism and, ultimately, cleptoparasitism. Cleptoparasitism evolved independently in Neotropical

Lestrimelitta and African *Cleptotrigona cubiceps*. Phylogenetic origins of these taxa are now being clarified. Some *Oxytrigona* attack other colonies and use their nests (Nogueira-Neto, 1997), as does *Tetragonisca angustula* (Sakagami et al., 1993; pers. obs.).

Nest dispersion, within a species, may be due to competition and anticipates uniform distribution among aggressive foraging species (Hubbell and Johnson, 1977; Breed et al., 1999) – provided suitable nesting sites are available. Colonies may battle over potential nesting sites (Hubbell and Johnson, 1977; Sakagami et al, 1993). *Lestrimelitta* regulate their colony densities by periodic contests (Sakagami et al., 1993), including pyrric battles, in which the raid costs many robbers' lives (Johnson, 1987, pers. obs.), or colony takeover of host nests, in which the entire host population is exterminated, but the robbers sustain little loss (Sakagami et al., 1993, pers. obs.). These and other authors observed that raiding *Lestrimelitta* also draw *Pseudohypocera* (phorid flies) to raided nests, which is against their interest – host nests are normally raided as sustainable resources.

The stasis of stingless bee nesting communities thus implies natural selection to reduce vulnerability to other stingless bee colonies, as outlined above, and also to avoid consequences of intense competition for food and nests that can lead to usurpation of nest sites, or cleptoparasitism.

6. COMMUNITY DYNAMICS

In natural vegetation, the stingless bee community, in terms of active nests, may number approximately 150 colonies in a square kilometer (100 ha), and the known range is from 15 to 1500 colonies, but varies considerably in biomass of colonies and bee size (Kajobe and Roubik, 2006; Samehima et al., 2004; Breed et al., 1999; Nogueira-Neto, 1997). Slight disturbance can change species composition (Brown and Albrecht, 2001). Unnatural human habitats have also yielded information on bee nest density (e.g. Michener, 1946; Morse, 1994). There are often many more nests in sites that are not extensive, intact old forest, but far fewer species, and possibly fewer adult bees (Batista et al., 2003; Eltz et al., 2003; Kajobe and Roubik, 2006). Individual species may have several hundred nests in a few hectares, but those are very small colonies. An estimate of 2 to 6 colonies ha^{-1} seems to apply to most larger or *detectable* colonies. Such resources for honey exploitation should be comparable to roughly one colony of *Apis mellifera* per hectare, 10 times the nesting density estimated for *A. mellifera* in tropical habitats (Kajobe and Roubik, 2006).

How often might stingless bee colonies reproduce, either by swarming or by having males fertilize queens? Remarkably, three studies done in Africa, America and Asia show annual mortality is 12 to 15% (Eltz et al., 2002; Kajobe and Roubik, 2006; Roubik and Harrison, pers. obs.). If and only if nests are continuously occupied, a stable local colony population with mortality of 13% means that about 5% ($.87^{22}$) of the original colonies are still living after 23 years. Thus, on average, a stingless bee colony can pass on its genes by reproducing in approximately a dozen years.

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Résumé – Biologie de la nidification des abeilles sans aiguillon. Par rapport au genre *Apis*, les abeilles sans aiguillon (Hymenoptera, Apidae, Meliponini) sont des sources variées et uniques de miel, avec 50 fois plus d'espèces et une origine qui remonte au Crétacé. Les reines s'accouplent une fois, les ouvrières n'ont pas d'aiguillon, les mâles butinent, la cire n'est pas le matériau primaire pour la construction et l'eau n'est pas utilisée pour refroidir les nids. Bien qu'on ignore pour la plupart la biologie de leur nidification, nous donnons ici une vue générale sur l'architecture, la défense et la maintenance des nids, la reproduction de la colonie, les symbiotes, les ennemis naturels et les associations animales dans le nid. La densité moyenne de colonies est de 150/km^2 dans les habitats naturels mais la biomasse des colonies et la taille des abeilles varie énormément. Il y a souvent plus de colonies dans les sites perturbés, par contre la richesse en espèces est bien moindre.

Les prédateurs comprennent des invertébrés, principalement des fourmis, et des vertébrés dont les chimpanzés qui utilisent des outils et les humains, ainsi que les ours, les mustélidés, les fourmiliers et de nombreux opportunistes. Parmi les parasites on trouve des mouches de la famille des phoridés néotropicales, quelques acariens mais peu de microbes connus. Les symbiotes des nids incluent des acariens fongivores, des coléoptères, des moisissures, des collemboles dans les latrines de la colonie, des coccidies qui fournissent de la cire et des acariens nécrophages. Les champignons et les bactéries mutualistes conservent la nourriture, fournissent des nutriments et écartent les parasites.

Contrairement à *Apis*, les abeilles sans aiguillon n'essaiment pas franchement (un nouveau site de nidification doit d'abord être préparé) et elles n'abandonnent pas leur nid. La reine n'effectue plus de vol une fois fécondée et les colonies ont apparemment une longue vie. L'adaptation est très visible dans les tubes d'entrée des nids, dans les plateformes propres aux espèces pour la défense du nid, dans le butinage et la ventilation. Les ouvrières ventilent avec leurs ailes et créent un courant d'air avec « des marées » qui renouvellent l'air du nid. Aux températures élevées, une moindre ventilation aide à maintenir une température fraîche dans le nid, mais le CO_2 augmente et est évacué la nuit. L'architecture est variable, en fonction de l'âge, du génotype et du microenvironnement, y compris les ennemis naturels. Les grands genres comme *Trigona, Melipona* et *Plebleia* ont une variabilité interspécifique considérable en ce qui concerne les sites de nidification, l'architecture et le comportement de défense, souvent lié à la vulnérabilité du nid. Le genre *Trigona* fabrique avec ses excréments une plaque, sorte de bouclier, qui lui procure défense et isolation, comme c'est le cas avec la terre, le bois, la résine ou les pierres pour les espèces qui nidifient dans le sol ou dans des cavités d'arbres. Une fine couche de surface sur les nids exposés permet en cas de rupture la sortie des abeilles qui défendent le nid et se mettent à mordre. On ne comprend pas actuellement le niveau d'évolution ni la phylogenèse du comportement de nidification. La disposition des cellules de couvain en chaînes reliées ou en amas ne semble pas liée particulièrement à la petite taille des abeilles. Les abeilles choisissent soigneusement leur mode de nidification et font preuve ainsi d'une adaptation particulière pour minimiser la vulnérabilité de la colonie aux ennemis naturels, à la compétition intraspécifique et à la cleptobiose. Elles conservent des liens durables entre la colonie mère et les colonies filles pour ce qui est de la nourriture et des reines vierges. Les reines ne s'accouplent qu'une fois et la mortalité de la colonie est de 13 % par an ; on peut donc prévoir une longévité de la colonie de 24 ans.

Meliponini / abeille sans aiguillon / nidification / architecture nid / micro-climat / écologie de l'évolution

Zusammenfassung – Nistbiologie bei Stachellosen Bienen. Im Vergleich zu den Honigbienen sind Stachellose Bienen sehr facettenreich und nutzen einzigartige Honigquellen, sie stellen 50 mal mehr Arten und entstanden bereits in der Kreidezeit. Die Königinnen paaren sich nur einmal, die Arbeiterinnen haben keinen Stachel, die Männchen suchen Futter, Wachs ist nicht das hauptsächliche Baumaterial und Wasser wird nicht zur Kühlung des Nestes benutzt. Obwohl die Nistbiologie meist unbekannt ist, wird hier eine allgemeine Sicht über Nestarchitektur, Verteidigung, Erhalt, Volksvermehrung, Symbionten, natürliche Feinde und Verhaltensmuster der Volksgemeinschaft gegeben. Unter natürlichen Umweltbedingungen beträgt die durchschnittliche Nestdichte 150/km^2, aber es leben dort verglichen mit veränderten Lebensräumen nur 1 % der Völker. In diesen gestörten Regionen gibt es zwar eine geringere Artenzahl, die aber unterschiedliche Biomasse aufweisen.

Feinde setzen sich aus Wirbellosen, vor allem Ameisen, und Wirbeltieren zusammen, einschließlich werkzeugbenutzenden Schimpansen, Menschen, Bären, Mardern, Ameisenbären und vielen Opportunisten. Als Parasiten kommen neotropische Buckelfliegen, einige Milben, aber nur wenige bekannte Mikroben vor. Als Symbionten kommen pilzverzehrende Milben und Käfer vor; in den Volkslatrinen gibt es Schimmelpilze und Springschwänze, im Nest Wachs erzeugende Schildläuse und Unrat vertilgende Milben. Mutuelle Pilze und Bakterien konservieren Futter, stellen Nährstoffe bereit und schalten Parasiten aus.

Im Gegensatz zu Honigbienen bilden Stachellose Bienen keine freien Schwärme und verlassen ihre Nester nicht. Die Königin fliegt nach Beginn der Eiablage nicht mehr. Ein neuer Nistplatz muss erst vorbereitet werden und Völker sind anscheinend langlebig. Besondere Anpassungen sind in den Röhren am Nesteingang zu erkennen, die artspezifische Plattformen für die Nestverteidigung, Sammelflüge und Ventilation darstellen. Arbeiterinnen schlagen die Flügel und erzeugen einen "Gezeiten" – Luftstrom, der die Luft im Nest erneuert. Bei hohen Temperaturen hilft vermindertes Fächeln eine kühlere Temperatur beizubehalten, aber der Gehalt an CO_2 steigt dann an und kann erst nachts entfernt werden. Die Architektur ist unterschiedlich, abhängig möglicherweise vom Alter, Genotyp und der die natürlichen Feinde einschliessenden Mikroumwelt. Große Arten wie *Trigona*, *Melipona* und *Plebeia* zeigen beachtliche innerartliche Varianzen in Lage und Architektur des Nestes und im Verteidigungsverhalten, das mit der Verletzlichkeit des Nestes zusammenhängt. *Trigona* formt mit ihren Exkrementen eine Deckplatte, die für Schutz und

Isolation sorgt, ähnlich wie Erde, Holz oder Steine bei anderen Arten, die in Erd- oder Baumhöhlen nisten. Eine schwache Oberflächenschicht bei freiliegenden Nestern ermöglicht den Austritt von verteidigenden, beißenden Bienen sowie diese zerbricht. Zur Zeit ist das Niveau der Evolution und die Phylogenie des Nistverhaltens noch nicht verstanden. Die Anordnung der Brutzellen in Ketten oder Gruppen scheint vor allem mit den kleinen Köpergrößen der Bienen zusammenzuhängen. Bienen suchen sich sorgfältig die Lage ihres Nestes aus und sind besonders angepasst, die Verletzlichkeit des Volkes gegen natürliche Feinde, innerartliche Konkurrenz und Räuberei zu minimieren. Sie halten in Bezug auf Nahrung und unbegattete Königinnen dauerhaft Verbindungen zwischen Mutter- und Tochterkolonien. Königinnen paaren sich nur einmal und die Volkssterblichkeit beträgt 13 % y^{-1}. Demnach berechnet sich die Überlebensdauer einer Kolonie auf 12 Jahre.

Meliponini / Apidae / Nestarchitektur / Nestmikroklima / evolutionäre Ökologie

REFERENCES

Akratanakul P. (1986) Beekeeping in Asia, F.A.O. Agric. Serv. Bull 68/4, Rome.

Amano K. (2005) Attempts to introduce stingless bees for the pollination of crops in green-house conditions in Japan, Food and Fertilizer Technology Center, Taipei, available at: http://www.fftc.agnet.org/library/article/tb167.html (accessed on 23 January 2006).

Antonini J., Martins R.P. (2004) The value of a tree species (*Caryocar brasiliense*) for a stingless bee *Melipona quadrifasciata quadrifasciata*, J. Insect Conserv. 7, 1671–1674.

Armbruster W.S. (1984) The role of resin in angiosperm pollination: ecological and chemical considerations, Am. J. Bot. 71, 1149–1160.

Baker E.W., Delfinado-Baker M. (1985) An unusual new species of *Neocypholaelaps* (Acari: Ameroseiidae) from the nests of stingless bees (Apidae: Meliponinae), Int. J. Acarol. 11, 227–232.

Batista M.A., Ramalho M., Soares A.E.E. (2003) Nesting sites and abundance of Meliponini (Hymenoptera: Apidae) in heterogeneous habitats of the Atlantic rain forest, Bahia, Brazil. Lundiana 4, 19–23.

Biesmeijer J.C., Giurfa M., Koedam D., Potts S.G., Joel D.M., Dafni A. (2005) Convergent evolution: floral guides, stingless bee nest entrances, and insectivorous pitchers, Naturwissenschaften, 92, 444–450.

Blomquist G.J., Roubik D.W., Buchmann S.L. (1985) Wax chemistry of two stingless bees of the *Trigonisca* group (Apidae: Meliponinae), Comp. Biochem. Physiol. 82, 137–142.

Breed M.D., McGlynn T.P., Sanctuary M.D., Stocker E.M., Cruz E. (1999) Distribution and abundance of selected stingless bee colonies in a Costa Rican tropical wet forest, J. Trop. Ecol. 16, 765–777.

Brown B.V. (1997) Parasitic phorid flies: a previously unrecognized cost to aggregation behavior of male stingless bees, Biotropica 29, 370–372.

Brown J.C., Albrecht C. (2001) The effect of tropical deforestation on stingless bees of the genus *Melipona* (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil, J. Biogeogr. 28, 623–634.

Buchwald R., Greenberg A.R., Breed M.D. (2005) A biomechanical perspective on beeswax, Am. Entomol. 51, 39–41.

Camargo J.M.F. (1970) Ninhos e biologia de algumas especies de meliponideos (Hymenoptera: Apidae) da região de Porto Velho, Territorio de Rondônia, Brasil, Rev. Biol. Trop. 16, 207–239.

Camargo J.M.F. (1984) Notas sobre habitos de nidificação de *Scaura* (*Scaura*) *latitarsis* (Friese) (Hymenoptera, Apidae, Meliponinae), Bol. Mus. Paraense E. Goeldi. 1, 89–95.

Camargo J.M.F., Wittmann D. (1989) Nest architecture and distribution of the primitive stingless bee, *Mourella caerulea* (Hymenoptera, Apidae, Meliponinae): evidence of the origin of *Plebeia* (s. lat.) on the Gondwana continent, Stud. Neotropic. Fauna Environ. 4, 213–229.

Camargo J.M.F., Roubik D.W. (1991) Systematics and bionomics of the apoid obligate necrophages: the *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae), Biol. J. Linn. Soc. 44, 13–39.

Camargo J.M.F., Pedro S.R.M. (l992) Systematics, phylogeny and biogeography of the Meliponinae (Hymenoptera, Apidae): a mini-review, Apidologie 23, 509–522.

Camargo J.M.F., Moure J.S. (1996) Meliponini neotropicais: o gênero *Geotrigona* Moure, 1943 (Apinae, Apidae, Hymenoptera), com especial referência à filogenia e biogeografia, Arq. Zool. São Paulo 33, 71–161.

Camargo J.M.F., Pedro S.R.M. (2002a) Mutualistic association between a tiny Amazonian stingless bee and a wax-producing scale insect, Biotropica 34, 446–451.

Camargo J.M.F., Pedro S.R.M. (2002b) Uma especie nova de *Schwarzula* da Amazonia, Iheringia, Ser. Zool. 92, 101–112.

Camargo J.M.F., Pedro S.R.M. (2003) Meliponini neotropicais: o genero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae) – bionomia e biogeografia, Rev. Bras. Entomol. 47, 311–372.

Camargo J.M.F., Pedro S.R.M. (2004) Meliponini neotropicais: o genero *Ptilotrigona* Moure (Hymenoptera, Apidae, Apinae), Rev. Bras. Entomol. 48, 353–377.

Camargo J.M.F., Roubik D.W. (2005) Neotropical Meliponini: *Paratrigonoides mayri*, new genus and species from western Colombia (Hymenoptera, Apidae, Apinae) and phylogeny of related groups, Zootaxa 1081, 33–45.

Cameron E.C., Franck P., Oldroyd B.P. (2004) Genetic structure of nest aggregations and drone congregations of the southeast Asian stingless bee *Trigona collina*, Mol. Ecol. 13, 2357–2364.

Cepeda-Aponte O.I., Imperatriz-Fonseca V.L., Velthuis H.H.W. (2002) Lesser wax moth *Achroia grisella*: first report for stingless bees and new capture method, J. Apic. Res. 41, 107–108.

Cortopassi-Laurino M., Nogueira-Neto P. (2003) Notas sobre a bionomia de *Tetragonisca weyrauchi* Schwarz, 1943 (Apidae, Meliponini), Acta Amaz. 33, 643–650.

Cruz-Landim C. da C. (1967) Estudo comparativo de algumas glândulas das abelhas (Hymenoptera, Apoidea) e respectivas implicações evolutivas, Arq. Zool. São Paulo, 15, 177–290.

Darchen R. (1972) Éthologie comparative de l'économie des matériaux de construction chez divers apids sociaux, *Apis*, *Trigona* et *Melipona* (Apidés), Rev. Comp. Anim. 6, 201–215.

Delfinado-Baker M., Baker E.W., Roubik D.W. (1983) New genus and species of Hypoaspidinae (Acari: Laelapidae) from nests of stingless bees, Int. J. Acarol. 9, 195–203.

Delfinado-Baker M., Baker E.W., Flechtmann C.H.W. (1984) Acari Domum Meliponinarum Brasiliensium Halitontes. 5. Two new genera and species of Laelapidae (Mesostigmata: Acari) from stingless bee nests, Int. J. Acarol. 10, 3–10.

Dollin A.E., Dollin L.J., Sakagami S.F. (1997) Australian stingless bees of the genus *Trigona* (Hymenoptera: Apidae), Invertebr. Taxon. 11, 861–896.

Drumond P.M., Bego L.R., Melo G.A.R. (1995) Nest architecture of the stingless bee *Plebeia poecilochroa* Moure and Camargo, 1993 and related considerations (Hymenoptera, Apidae, Meliponinae), Iheringia, Ser. Zool., Porto Alegre 79, 39–49.

Eardley C.D. (2004) Taxonomic revision of the African stingless bees (Apoidea: Apidae: Apinae: Meliponini), African Plant Protection 10, 63–96.

Eickwort G.C. (1990) Associations of mites with social insects, Annu. Rev. Entomol. 35, 469–488.

Eltz T., Bruhl C.A., Kaars S. van der, Linsenmair K.E. (2002) Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia, Oecologia 131, 27–34.

Eltz T., Bruhl C.A., Imiyabir Z., Linsenmair K.E. (2003) Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests of Sabah, Malaysia, with implications for forest management, For. Ecol. Manage. 172, 301–313.

Engels W., Rosenkranz P., Engels E. (1995) Thermoregulation in the nest of the Neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees, Stud. Neotrop. Fauna Environ. 30, 193–205.

Franck P., Cameron E., Good G., Rasplus J.-Y., Oldroyd B.P. (2004) Nest architecture and genetic differentiation in a species complex of Australian stingless bees, Mol. Ecol. 13, 2317–2331.

Garcia M.V.B., Oliveira M.L., Campos L.A.O. (1992) Use of seeds of *Coussapoa asperifolia magnifolia* (Cecropiaceae) by stingless bees in the central Amazonian forest (Hymenoptera: Apidae: Meliponinae), Entomol. Gen. 17, 255–258.

Gilliam M., Roubik D.W., Lorenz B.J. (1990) Microorganisms associated with pollen, honey, and brood provisions in the nest of a stingless bee, *Melipona fasciata*, Apidologie 21, 89–97.

Goulson D. (2003). Bumblebees: behavior and ecology, Oxford, UK.

Hansell M.H. (1993) The ecological impact of animal nests and burrows, Funct. Ecol. 7, 5–12.

Hepburn H.R., Kurstjens S.P. (1984) On the strength of propolis (bee glue), Naturwissenschaften 71, 591–592.

Hubbell S.P., Johnson L.K. (1977) Competition and nest spacing in a tropical stingless bee community, Ecology 58, 949–963.

Inoue T., Sakagami S.F., Salmah S., Nukmal N. (1984) Discovery of successful absconding in the stingless bee *Trigona* (*Tetragonula*) *laeviceps*, J. Apic. Res. 23, 136–142.

Johnson L.K. (1987) The pyrric victory of nest-robbing bees: did they use the wrong pheromone? Biotropica 19, 188–189.

Johnson L.K., Hubbell S.P. (1986) Nest tree selectivity and density of stingless bee colonies in a Panamanian forest, in: Chadwick A.C., Sutton S.L. (Eds.), Tropical Rain-Forest: The Leeds Symposium, Leeds Phil. Soc., Leeds, UK, pp. 147–154.

Kajobe R., Roubik D.W. (2006) Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve, Biotropica 38, 210–218.

Kerr A.S., Kerr W.E. (1999) *Melipona* garbage bees release their cargo according to a Gaussian distribution, Rev. Bras. Biol. 59, 119–123.

Kerr W.E., Sakagami S.F., Zucchi R., Portugal Araújo V., Camargo J.M.F. (1967) Observações sobre a arquitetura dos ninhos e comportamento de algumas especies de abelhas sem ferrão das vizinhanças de Manaus, Amazonas (Hymenoptera, Apoidea), Atlas do simpôsio sobre a biota Amazônica 5, 255–309.

Kistner D.H. (1982) The social insects' bestiary, in: Hermann H.R. (Ed.), Social Insects, Vol. III, Academic Press, New York, pp. 2–244.

Koedam D., Jungnickel H., Tentschert J., Jones G.R., Morgan E.D. (2002) Production of wax by virgin queens of the stingless bee *Melipona bicolor* (Apidae, Meliponinae), Insectes Soc. 49, 229–233.

Kolmes S.A., Sommeijer M.J. (1992) Ergonomics in stingles bees changes in intranidal behavior after partial removal of storage pots and honey in *Melipona favosa* (Hymenoptera: Apidae; Meliponinae), Insectes Soc. 39, 215–232.

Langenheim J. (2003) Plant resins. Chemistry, evolution, ecology, ethnobotany, Timber Press, Portland Oregon.

Lokvam J., Braddock J.F. (1999) Anti-bacterial function in the sexually dimorphic pollinator rewards of *Clusia grandiflora* (Clusiaceae), Oecologia 119, 534–540.

Macieiera O.J.D., Proni E.D. (2004) Capacidade de resistência a altas e baixas temperaturas em operárias de *Scaptotrigona postica* (Latreille) (Hymenoptera, Apidae) durante os períodos de verão e inverno, Rev. Bras. Zool. 21, 293–296.

Martins C.F., Cortopassi-Laurino M., Koedam D., Imperatriz-Fonseca V.L. (2004) Tree species used for nidification by stingless bees in Brazilian Caatinga, Biota Neotropica v4n2/en/BN00104022004.

Melo G.A.R. (1996) Notes on the nesting biology of *Melipona capixaba* (Hymenoptera, Apidae), J. Kans. Entomol. Soc. 69, 207–210.

Michener C.D. (1946) Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae), J. N.Y. Entomol. Soc. 54, 179–197.

Michener C.D. (1959) Sibling species of *Trigona* from Angola (Hymenoptera, Apidae), Am. Mus. Novit. 1956, 1–5.

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

Michener C.D. (1974) The social behavior of the bees: a comparative study, Belknap, Harvard University Press, Cambridge.

Michener C.D. (2000) Bees of the world, Johns Hopkins Press, Baltimore.

Michener C.D. (2001) Comments on minute Meliponini and the male of the genus *Pariotrigona* (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 74, 231–236.

Moritz R.F.A., Crewe R.M. (1988) Air ventilation in nests of two African stingless bees *Trigona denoiti* and *Trigona gribodoi*, Experientia 44, 1024–1027.

Morse R.A. (1994) The new complete guide to beekeeping, The Countryman Press, Woodstock, Vermont.

Nogueira-Neto P. (1948) Notas bionomicas sobre meliponineos. I. Sobre ventilação dos ninhos e as constucões com ela relationadas, Rev. Bras. Biol. 8, 465–488.

Nogueira-Neto P. (1949) Notas bionomicas sobre meliponineos. II. Sobre a pilhagem. Papeis Avulsos do depto. De Zoologia da Secr. Agr. Do Est. De São Paulo, pp. 13–32.

Nogueira-Neto P. (1962) The scutellum nest structure of *Trigona* (*Trigona*) *spinipes* Fab. (Hymenoptera: Apidae), J. N.Y. Entomol. Soc. 70, 239–264.

Nogueira-Neto P. (1970) A criaçao de abelhas sem ferrao (1st ed., 1953), Chacaras e Quintais, Sao Paulo.

Nogueira-Neto P. (1997) Vida e criaçao de abelhas indigenas sem ferrao, Editora Nogueirapis, Sao Paulo.

Oliveira M.L., Morato E.F., Garcia M.V.B. (1995) Diversidade de espécies e densidade de ninhos de abelhas socias sem ferrão (Hymenoptera, Apidae, Meliponinae) em floresta de terra firma na Amazônia central, Rev. Bras. Biol. 12, 13–24.

Palmer K.A., Oldroyd B.P., Quezada-Euan J.G., Paxton R., May-Itza W. de. J. (2002) Paternity frequency and maternity of males in some stingless bee species, Mol. Ecol. 11, 2107–2113.

Paxton R.J., Bego L.R., Shah M.M., Mateus S. (2003) Low mating frequency of queens in the stingless bee *Scaptotrigona postica* and worker paternity of males, Behav. Ecol. Sociobiol. 53, 174–181.

Peck S.B. (2003) The eyeless inquiline genera *Parabystus* and *Scotocryptus* of Costa Rica and Panama; inhabitants of nests of stingless bees (Coleoptera: Leiodidae), Sociobiology 42, 65–80.

Peruquetti R.C., Dias Bezerra J.M. (2003) Inquilinos de abelhas-sem-ferrão (Hymenoptera: Apidae): aspectos da biologia de *Scotocryptus melitophilus* Reitter, 1881 (Coleoptera: Leiodidae), Entomotropica 18, 215–218.

Peters J., Queller D.C., Imperatriz-Fonseca V.L., Roubik D.W., Strassmann J.E. (1999) Mate number, kin selection and social conflicts in stingless bees and honeybees, Proc. R. Soc. London B 266, 379–384.

Platnick N.I., Shadab M.U. (1981) On Central American *Cryptocellus* (Arachnida, Ricinulei), Am. Mus. Novit. 2711, 1–21.

Portugal-Araújo V. (1955) A contribution to the bionomics of *Lestrimelitta cubiceps* (Hymenoptera, Apidae), J. Kans. Entomol. Soc. 31, 203–211.

Portugal-Araújo V. (1958) Notas sobre coloinas de meliponineos de Angola, Dusenia 6, 97–114.

Posey D.A., Camargo J.M.F. de (1985) Additional notes on the classification and knowledge of stingless bees (Meliponinae, Apidae, Hymenoptera) by the Kayapó Indians of Gorotire, Pará, Brazil, Ann. Carnegie Mus. 54, 247–274.

Rasmussen C. (2004) A stingless bee nesting with a paper wasp (Hymenoptera: Apidae, Vespidae), J. Kans. Entomol. Soc. 77, 593–601.

Roubik D.W. (1979) Nest and colony characteristics of stingless bees from French Guiana (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 52, 443–470.

Roubik D.W. (1981) A natural mixed colony of *Melipona* (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 54, 263–268.

Roubik D.W. (1983) Nest and colony characteristics of stingless bees from Panama, J. Kans. Entomol. Soc. 56, 327–355.

Roubik D.W. (1989) Ecology and natural history of tropical bees, Cambridge University Press, New York.

Roubik D.W. (1992) Stingless bees (Apidae: Meliponinae): a guide to Panamanian and Mesoamerican species and their nests, in: Quintero D., Aiello A. (Eds.), Insects of Panama and Mesoamerica, Oxford University Press, Oxford, UK, pp. 495–524.

Roubik D.W. (1993) Direct costs of forest reproduction, bee-cycling and the efficiency of pollination modes, J. Biosci. 18, 537–552.

Roubik D.W., Wheeler Q. (1982) Flightless beetles and stingles bees: phoresy of scotocryptine beetles on their meliponine hosts, J. Kans. Entomol. Soc. 55, 125–135.

Roubik D.W., Peralta F.A.P. (1983) Thermodynamics in nests of two *Melipona* species in Brasil, Acta Amaz. 13, 453–466.

Roubik D.W. Moreno J.E., Vergara C., Wittmann D. (1986) Sporadic food competition with the African honey bee: projected impact on neotropical social bees, J. Trop. Ecol. 2, 97–111.

Roubik D.W., Yanega D., Aluja-S. M., Buchmann S.L., Inouye D.W. (1995) On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae), Apidologie 26, 197–211.

Roubik D.W., Sakai S., Hamid Karim A.A. (Eds.) (2005) Pollination ecology and the rain forest: Sarawak Studies, Springer Ecological Studies No. 174, Springer Sciences + Business Media Inc., New York.

Sakagami S.F. (1982) Stingless bees, in: Herman H.H. (Ed.), Social insects, Vol. III, Academic Press, New York, pp. 361–423.

Sakagami S.F., Yamane S., Hambali H.G. (1983a) Nests of some southeast Asian stingless bees, Bull. Fac Education, Ibaraki Univ. (Nat. Sci.) 32, 1–21.

Sakagami S.F., Inoue T., Yamane S., Salmah S. (1983b) Nest architecture and colony composition of the Sumatran stingless bee *Trigona* (*Tetragonula*) *laeviceps*, Kontyû 51, 100–111.

Sakagami S.F., Inoue T., Yamane S., Salmah S. (1989) Nests of the myrmecophilous stingless bee, *Trigona moorei*: how do bees initiate their nests within an arboreal ant nest? Biotropica 21, 265–274.

Sakagami S.F., Roubik D.W., Zucchi R. (1993) Ethology of the robber stingless bee, *Lestrimelitta limao* (Hymenoptera: Apidae), Sociobiology 21, 237–277.

Samejima H., Marzuki M., Nagamitsu T., Nakashizuka T. (2004) The effects of human disturbance on a stingless bee community in a tropical rainforest, J. Biol. Conserv. 120, 577–587.

Schwarz H.F. (1948) Stingless bees (Meliponidae) of the Western Hemisphere, Bull. Am. Mus. Nat. Hist. 90, 1–546.

Smith B.H., Roubik D.W. (1983) Mandibular glands of stingless bees (Hymenoptera: Apidae): chemical analysis of their contents and biological function in two species of *Melipona*, J. Chem. Ecol. 9, 1465–1472.

Smith NG. (1968) The advantage of being parasitized, Nature 219, 690–694.

Starr C.K., Sakagami S.F. (1987) An extraordinary concentration of stingless bee colonies in the Philippines, with notes on nest architecture (Hymenoptera: Apidae: *Trigona* spp.), Insectes Soc. 34, 96–107.

Teixeira C.P., et al. (2003) *Starmerella meliponinorum* sp. nov., a novel ascomycetous yeast species associated with stingless bees, Int. J. Syst. Ecol. Microbiol. 53, 339–343.

Velthuis H.W., Koedam K., Imperatriz-Fonseca V. (2005) The males of *Melipona* and other stingless bees, and their mothers, Apidologie 36, 169–185.

Wallace H.M., Trueman S.J. (1995) Dispersal of *Eucalyptus torelliana* seeds by the resin-collecting stingless bee, *Trigona carbonaria*, Oecologia 104, 12–16.

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

Wille A., Michener C.D. (1973) The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera: Apidae), Rev. Biol. Trop. Suppl. 21, 9–278.

Wille A., Orozco E. (1975) Observations on the founding of a new colony by *Trigona cupira* (Hymenoptera: Apidae) in Costa Rica, Rev. Biol. Trop. 22, 253–287.

Wittmann D. (1989) Nest architecture, nest site preferences and distribution of *Plebeia wittmanni* (Moure and Camargo, 1989) in Rio Grande do Sul, Brazil (Apidae: Meliponinae), Stud. Neotrop. Fauna Environ. 24, 17–23.

Wittmann D., Radtke R., Zeil J., Lubke G., Francke W. (1990) Robber bees (*Lestrimelitta limao*) and their host chemical and visual cues in nest defense by *Trigona* (*Tetragonisca*) *angustula* (Apidae: Meliponinae), J. Chem. Ecol. 16, 631–641.

Zucchi R., Sakagami S.F. (1972) Capacidade termoreguladora em *Trigona spinipes* e em algumas outras aspecies de abelhas sem ferrão, in: Homenagem a W.E. Kerr, Rio Claro, Brasil, pp. 301–309.