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The role and significance of stingless bees (Hymenoptera: Apiformes: Meliponini) in the natural environment

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Abstract
This article refers to the biology and ecology of stingless bees (Meliponini), living in tropical and subtropical areas. Similar to honey bees (*Apis mellifera*), stingless bees (Meliponini) belong to the category of proper social insects and are at the highest level of social development. This group of insects comprises about 500 species and they are the most common bees pollinating the native plants in many tropical areas. Families of stingless bees are usually quite numerous, reaching up to 100,000 individuals. They are characterised by polymorphism, age polyethism and perennialism. This article presents the structural complexity of natural nesting of these tropical insects and their ability to settle in artificial nest traps. The main significance of stingless bees for humans is their role in the natural environment as pollinators, which is an essential factor influencing biodiversity.

1. INTRODUCTION

Bees (Apiformes) represent a very important element influencing biodiversity; as active pollinators. They play a key role in maintaining the species richness of many plants [Jennersten et al., 1991; Kearns et al., 1998; Williams et al., 2001; Cussans et al., 2010]. These insects belong to specialised phytophages, pollinating over 70% of plant species [Richards, 1986]. They appeared in Earth's history in the Cretaceous period along with angiosperm plants, and thus, are considered a relatively young insect group. They visit flowers for the collection of nectar and pollen, which they consume. So far, the occurrence of almost 16,000 bees has been determined worldwide. However, most scientists, including Michener [2007], assume that this number must be much higher, even above 30,000 species. Bees are a monophyletic group, which evolved from flower-visiting wasps, most probably the ancestors of the Sphecoidea. For example, Brothers (1975) and others link the Sphecoidea and bees in the Superfamily Apoidea, distinguishing two sections: the Spheciformes and the proper bees, also known as the Apiformes.
Michener [2007] distinguished 10 families within the Apiformes. Families occurring outside Europe include bees, whose dwelling is restricted to specific regions, for example, Australian (family Stenotritidae), Neoarctic (family Oxaeidae) and tropical areas (families Fidellidae and Ctenoplectridae). Similarly, as in Europe, representatives of 6 families occur in Poland: Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae and Apidae; the latter includes the Anthophoridae. The most well-known family is the Apidae, to which belongs the most 'popular' bee *Apis mellifera* (European honey bee). The family also contains the tribe Euglossini (orchid bees), living in tropical areas of the New World and being the only bees of the family that are not properly social. The Apidae also contain the stingless bees (Meliponini), living in the tropical and subtropical areas. The southern range of the stingless bees reaches the 25 latitude, whereas the northern range reaches the Tropic of Cancer (Fig. 1).

Apiologists present a view that the oldest bees appeared in the early mid-Cretaceous, that is, about 125 million years ago. From that time onwards, they co-evolved with angiosperms. Till recently, it was considered that the oldest (preserved in amber) species is the worker *Trigona prisca* representing a stingless bee from the genus *Trigona* from the Cretaceous. It was found in New Jersey, USA, and was described by Michener and Grimaldi [1988].In 2006, however, George Poinar discovered *Melittosphex burmensis* from amber found in the Lower Cretaceous strata of northern Myanmar. This insect, about 3 mm in

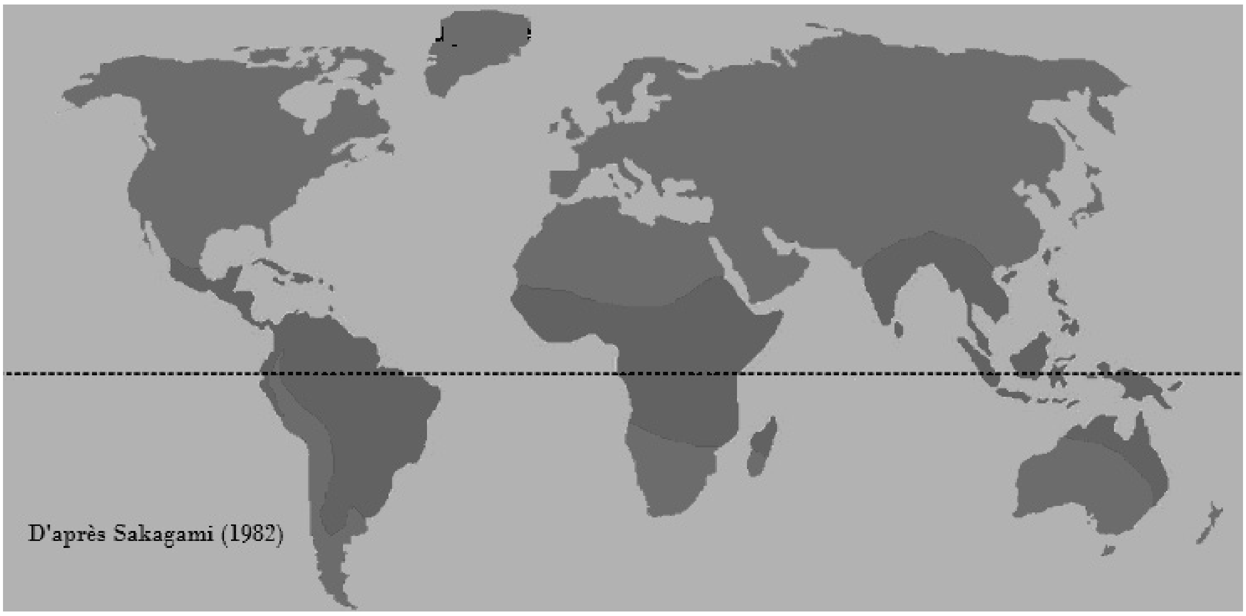

Figure 1. Distribution of Meliponini (shaded areas) (http://www.encyclopedie-universelle.net)

size, shows features transitional between bees and wasps, and is presently considered the oldest described fossil bee [Poinar and Danforth, 2006].

2. GENERAL CHARACTERISTICS OF STINGLESS BEES

It is commonly considered that stingless bees (Meliponini) are derived from Africa. However, Kerr and Maule [1964] evidence a much higher diversity of this group in South and Central America; their wide distribution in the Miocene points to the origin of these bees in South America prior to the drowning of the Panama Isthmus in the early Eocene.
Meliponini are a large group comprising about 500 species; in many tropical areas, these are the most common bees, playing the main role in pollinating native plants. According to Kerr and Maule [1964], the tropical areas of the New World contain 183 species, Africa – 32 species, Asia – 42, and Australia and New Guinea – 20 species of these insects. Due to the behavioural complexity, diversity and abundance, the Meliponini are presently the most commonly studied group in America. Results of these investigations are presented each year in seminars in Brazil, during which 40% from about 260 reports are focused on the Meliponini [Garófalo and Freitas, 2002].
Fifty-six genera were distinguished within the Meliponini, among which, three are most common. They include: *Melipona* from the tropical areas of South America, *Meliponula* from the tropical areas of Africa (Fig. 2) and *Trigona*, documented in the tropical areas of the mentioned continents. Of economic significance are the species of the genera *Melipona* and *Trigona* [Camargo, 1996].

Figure 2. Meliponula ferruginea (photo by Muhammad Mahdi Karim)

The common name of these insects – stingless bees – comes from the fact that bees of this group have highly reduced stingers, which are not used for defence. The workers of most species of stingless bees effectively defend themselves against enemies by roaming around the attacker's body, stinging it with mandibles, pulling hair and clasping the mandibles within it. Release of this clutch requires detaching of the head from the insect's body. The tropical *Trigona flaveola* from South America secretes a burning liquid from its mandibles (formic acid in the subfamily Oxytrigina), which in Brazil has given this species the name '*caga-fogos*', that is 'flamethrowers' or 'fiery bees'. Stingless bees fight very effectively with other insects.

3. MORPHOLOGY OF STINGLESS BEES

The size of these insects varies from 16 mm (in a worker of the genus *Trigona*) to about 2 cm in the species of *Melipona*. They are black to golden in colour; some species have shiny bodies, whereas others are covered with hair. The body of bees from the tribe Meliponini comprises three parts – the head (cephalon), the trunk (thorax) and the abdomen. The head contains a pair of antennae, a pair of compound eyes, simple eyes and chewing-sucking mouthparts. The thorax bears two pairs of membranous wings and three pairs of legs. Bees as the only hymenopterids have the ability to collect pollen. The pollen apparatus in the Meliponini is a basket located on the hind legs. The pollen basket is built of long, thick hairs, surrounding the external, non-hairy, concave and smooth surface of the hind legs. The hairs hold a pollen lump, stuck to the hind legs and forming the pollen trap. Bees feed on plant pollen and nectar. Depending on the species, they may fly as far as 2 km from their nests. Some representatives of the Meliponini collect resin from tree trunks and branches. A completely different feeding strategy occurs in three species of the Melipolini from the *Trigona hypogea* group. Workers of these bees feed their larvae with partly digested tissues of dead vertebrates [Kwapong et al., 2010].

4. SOCIAL LIFE OF STINGLESS BEES

The superfamily Apoidea includes solitary, pre-social, properly social and parasite bees. All the stingless bees (Meliponini) belong to properly social bees, characterised by the following features: representatives of one species jointly nurse the offspring; there is a reproduction work subdivision, that is, a caste system; and at least two generations are capable of work for the whole family, that is, the offspring help the parents in raising their own siblings.

Meliponini usually form large families, reaching over 10,000 to even 100,000 or more individuals in number, and according to Michener [Michener,2007]are the most social bees. Similarly, as the honey bee *Apis mellifera*, and contrary to other bees, they live in stable families and display morphological and behavioural variability.

Similarly, as honey bees, Meliponini are characterised by stable polymorphism. Apart from a typical female form, the queen and a worker, which is a female with reduced reproductive organs, there is also a male drone. The social organisation within a single family includes one queen, several hundred drones and several thousand workers. The weight of the Meliponini queen is similar to that of a worker, but its thorax and cephalon are smaller, being equalized by the large abdomen. During its life, the queen feeds, copulates and lays eggs, never helping the workers in their everyday work with nest construction, raising the offspring and getting food [Kwapong et al., 2010].

Stingless bees are characterised by age polyethism. It is partly related with the activity of external glands. Division of labour among the workers depends on organised behaviour change taking place during the bee's life [Sakagami, 1982]. Stingless bees possess an advanced system of chemical alarming and informing, enhanced by a modulated sound signal, that is, buzzing. The length of sound oscillations increases with the covered distance. Upon finding food, workers of Meliponini alarm the remaining bees very fast by smell traces [Lindauer and Kerr, 1960].This is a very effective method of information in tropical forests. After collecting food, on its way to the nest, the bee stops every few meters on plants or on the ground, leaving a drop of secretion from its mandible glands. The smell traces of stingless bees are polarised so that larger amounts of the smelling substance are located closer to the food source. Smell traces of the Meliponini are far more advanced than the honeybee's dance (*Apis mellifera*), which has the same purpose, that is, showing the way to the food source. The honeybee's dance transfers the information in two dimensions, by showing the position of the point on a plane, whereas the smell trace in the Meliponini by leading up and down provides a three dimensional information [Wilson, 1979].

5. LIFE CYCLE

Families of stingless bees can live perennially and reproduce by swarming. The life cycle begins when scout bees, probably aroused by high density in the old nest, begin to find a locality for a new nest. When the new locality is chosen, the workers seal all openings around the fracture in the ground and construct a nest entrance. At first, the building material is taken from the old nest. The workers collect beeswax in baskets located on the third pair of legs, and carry honey and pollen as fluid suspension in their goitres. At the same time, groups of males gather around the new nest. The new queen raised by the workers lives in the old nest for some time with the mother queen. Next, the new queen flies to the new nest alone or surrounded by a group of bees; soon, it performs the mating dance, which, for example, in *Melipona quadrifasciata* lasts for about 4 to 5 minutes.

When comparing the reproduction of stingless bees (Meliponini) and honeybees (*Apis mellifera*), that is, insects characterised by the highest level of social development, Wilson [Wilson, 1979]showed two main differences. In honeybees, separation of a new family is fast and complete – the swarm leaves the family nest, dragging the new queen, sits for a short time on a nearby branch forming the 'swarm cluster', and then migrates to the new nest. Most probably, the tracker bees had visited the locality selected for the new nest. In turn, in Melipononi, there is a strong bond between the home nest and the offspring nest, and the formation of a new family is gradual. The new queen of stingless bees migrates to a new nest, already organised by the workers. In *Apis mellifera*, it is the old queen that migrates, whereas in Meliponini the new queen moves to the new nest, the old queen being incapable of flight having a heavy abdomen and frayed wings. The development stages of stingless bees include:

a larva known as maggot, a pupa and an adult individual (imago).

6. NEST CONSTRUCTION IN STINGLESS BEES

The nest construction in the Meliponini is complex, characterised by a variable structure, and thus, suitable for evolutionary interpretation. Most species nest in various natural cavities in the ground, hollow trunks and tree branches, dead wood, abandoned ant and termite nests, and animal burrows, fractures in stone walls or caves. The species *Dectylurina staudingeri* and *Dectylurina schmidti* build their spherical nests high in the trees attached to branches.

In Meliponini, the construction of nest entrances also depends on the species. Some stingless bees construct simple nest entrances, whereas other build copula-like entrances in the form of rosettes (e.g., *Trigona flavicornis*) or trumpet-shaped entrance platforms (e.g., *Hypotrigona* sp.). Species of *Trigona* cover the entrance with sticky propolis (bee glue), effectively discouraging ants and other insects [Roubik, 2006]. The nests are usually built of cerumen (beeswax), which is a brown-coloured mixture of wax and propolis. Sand or mud may be added to the cerumen.

In the simplest case, the nest of stingless bees resembles the nest of bumblebees (*Bombus*), as in the case of *Hypotrigona gribodoi*. It is composed of an internal grouping of larval cells, which may form compact combs or occur as compact bunches. The cells are open upwards and sealed after the eggs are laid. After usage, the cells are destroyed. The cells are surrounded by large, egg-shaped pots used for storing honey and pollen.

In a *Melipona pseudocentris* and *Meliponula bocandei* nest situated in a hollow tree trunk, the larval cells are regularly arranged in a comb-like horizontal structure. They are separated by wax pillars also called connectors. Identical supplementary pots built of soft beeswax are located above and used for storing honey and pollen.

Larval cells in which single individuals develop are surrounded by a soft beeswax cover (involucrum). Its role is to maintain a stable temperature in the nest. The involucrum is composed of several sheets and the bees move around in free spaces.

Larval cells and pots with honey and pollen are protected by an external, very thick and hard cover (bitumen) composed of propolis, hard beeswax, often plant substances, mud and so on. The cover may be multi-layered, with the bees moving around in the free spaces.

In underground nests, for example, *Trigona testacea*, the nest entrance is terminated with a several centimetres long entrance pipe, which may be built of pure wax. An over 10 cm long entrance corridor leads to the nest chamber. The supply pots are located under the larval cells [Wilson, 1979]. Based on numerous observations, Michener [2007] assumed that pure wax is used by stingless bees only in rare cases and only for the most external parts of the entrance pipe or as wall covers of the entrance corridor. All species of stingless bees guard the nest entrance against intruders. This task is performed by a few to over 10 workers. During the night, workers guarding the nest entrance draw back and seal the entrance. The propolis sealing is removed each morning and built again in the evening [Kwapong et al., 2010].

The ability of settling of some wild bees in artificial nests, that is, nest traps, was used in artificial cultivation for economic use. Clay and wooden traps are usually situated near human dwellings and are found in many parts of the worlds, for example, Borneo, Mexico or Indonesia.

7. ROLE OF STINGLESS BEES IN THE ENVIRONMENT

Plant reproduction by pollination, including crops, forest trees, bushes and herbs is indispensable for further existence of an ecosystem; bees of various species play a crucial role in this process, which results in the quantity and quality of fruit and seeds in over 70% of flowering plants. Stingless bees play a key role in pollinating native flora in tropical areas. A plant species from the orchid group – vanilla (the most valuable spice after saffron) – is pollinated in Mexico exclusively by stingless bees from the genera *Trigona* and *Melipona*. Insects of this group pollinate such plants as: macadamia, mango, strawberries, watermelons, avocado, citrus plants, lychee and many others. Meliponini are also used to pollinate greenhouse plants. In Australia, *Meliplebeia beccari* pollinates greenhouse tomatoes, whereas *Melipona quadrifasciata* works much more efficiently in the Brazilian greenhouses than *Apis* sp.

Honey produced by stingless bees is aromatic, sweet-sour in taste with a fruity tint. It contains more water (about 20-35%) and is more liquid than the honey produced by honeybees [Vit et al., 2004].In the Yucatan Peninsula lives the bee *Melipona beecheii*, which in the Maya language is known as '*kab*'. Honey of these bees is used in local medicines and religious rituals and ceremonies [Ocampo-Rosales, 2013].However, honey collected from some bee species is not edible due to the admixture of inedible substances of plant origin. From 1 to 1.5 kg of honey can be obtained from one family of Meliponini. Other products obtained from Meliponini include:

- propolis, which has been examined and proven to be effective in the treatment of many health problems, that is, infections and wound healing, and has antibiotic properties;
- pollen, which is rich in vitamins, proteins and mineral components, and is used in the production of many cosmetics;
- beeswax is used in the production of numerous industrial products and in pharmaceutics.

8. SUMMARY

All the presented specific features of the behaviour of bees from the tribe Meliponini clearly indicate that these represent insects at the highest level of social evolution, even exceeding that of honeybees. It is commonly assumed that the social organisation of these insects developed after the separation of the ancestors of the present-day tribes of Meliponini and Apini. Their role in plant pollination indicates high economic significance of these tropical insects.

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