



Stingless Bees of Pará

Based on the Scientific Expeditions
of João M. F. Camargo

Editors

Vera L. Imperatriz-Fonseca
and Denise A. Alves



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Foreword

JOSÉ OSWALDO SIQUEIRA

Director of the Instituto Tecnológico Vale – Desenvolvimento Sustentável (ITV-DS)

There are many species of stingless bees in Brazil, especially in the Amazon, a region that requires more scientific knowledge about these social insects. In the literature, there are usually few references to their nests, life habits and products, such as honey, resins, cerumen and pollen. Information related to the use of stingless bee colonies by the pre-Columbian peoples of the Americas shows many points in common among the various ethnic groups. When evaluating the global biocultural aspects, there is often a similar basis in this recognition of bees and their products, such as medicines, offerings, importance in the social hierarchy, commercial use, and ecological role.

The scientific expeditions conducted by João M. F. Camargo to the Amazon, in search of native stingless bees' nests, allowed the identification of new information on one of the most biodiverse ecosystems in the world and its peculiarities. The photographic record of the nests of these social bees, as compiled in this publication, allows us to reflect on new biocultural horizons.

The idealization of this book allowed the gathering of both the information valued by scientific publications and the care with which this record was made and organized in an entomological reference collection at the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto of Universidade de São Paulo. The retrieval of some of this information was made possible by digitizing Prof. João M. F. Camargo's photo library, which will certainly contribute to the identification of species of bees whose nests are rescued in areas of authorized plant suppression, as occurs in a legal and responsible manner in Carajás National Forest and many other ventures.

At a time when the whole world is concerned with the decline in bee populations, we illustrate here the biodiversity of stingless bees in the Amazon, especially in Carajás, in the state of Pará. This is a relevant work for the communities in the region that are increasingly interested in the rearing and sustainable use of social bees, which generates income and thus socio-environmental development.

Preface

HUGO BARRETO


Director of Sustainability and Social Investment of Vale

Biological collections are dynamic and permanent sources of knowledge on biodiversity: they provide essential information on the morphological and genetic components of species diversity, and geographic distribution records, among other important aspects of diversity. Often, they are the only archive of extinct species, which makes them essential for the development of scientific research on biodiversity. Information that has been collected over many decades is vital to define priority areas for research and conservation as well as for the identification of understudied taxa, among other functions.

We know how collaborative work brings better outcomes and consolidates new opportunities. In this sense, the publication *Stingless bees of Pará* is a reference, in that it gathers the results of scientific expeditions to the Amazon with a focus on the occurrence and distribution of stingless bees and their nests, collaborations between researchers and alliances that have been established among institutions.

It also celebrates the activities of researchers, who were transformative figures, i.e., that produced works of extraordinary quality, and which traverse the boundaries of science and art: Warwick E. Kerr, a great scientist who pioneered bee studies in the Amazon, the taxonomist João M. F. Camargo, the anthropologist Darrell A. Posey and Kwyrà-Kà, the bee expert of Gorotire Village. Together, they illuminated, for example, the vast wealth of traditional knowledge on bees of the Kayapó people, which domesticated nine bee species, among the 56 that they knew by name and utilised in everyday activities.

The results of this collaborative action, including researchers from Instituto Tecnológico Vale (ITV), is what is shared here for the purpose of creating opportunities for the generation of knowledge on the sustainable use of natural resources, based on the triad of research, education and entrepreneurship. By making this selection available, we also sought to mobilize society on the urgency of preserving biological collections and encourage the discovery of new horizons for the sustainable use and conservation of natural resources.

A pencil sketch of a tree trunk and branches with leaves, set against a dark teal background. The drawing is done in a simple, expressive style with visible pencil lines. The tree trunk is the central focus, with several branches extending outwards, some bearing leaves. The background is a solid, dark teal color.

*In memory of João M. F. Camargo,
Darrell A. Posey, and Warwick E. Kerr.
They were transforming scientists
who crossed the barriers of knowledge
and built bridges between different
fields through their integrative way of
scientific thinking.*

Prologue

The stingless bees (Meliponini) in the Amazonian Region were carefully studied by João Maria Franco de Camargo during his expeditions to the Amazon between 1963-2001, when he covered 16,000 km of waterways. This great naturalist was also an amazing artist and observer. Self-taught and expert with remarkable knowledge, he deeply knew the social bees of Brazil. Therefore, in 1976, he was accepted for a Master's degree at the Universidade Federal do Paraná, guided by the studies on bee taxonomy of Father Jesus S. Moure. His abilities defined him as one of the great naturalists of bees of the twentieth century, whose work included data obtained in the field and subsequent publications, as well as the collection designed by him and implemented by the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto of Universidade de São Paulo (FFCLRP-USP), where he was a professor. Deceased in 2009, the contribution of João Camargo was also evidenced in the 'Meliponini' section published in the Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region, when he reviewed, with his collaborator Silvia R. M. Pedro, all the existing scientific literature on the species of stingless bees in the Neotropical Region until 2004, including comments on the taxonomic identifications of the species.

João Camargo made several expeditions to the Amazon, where he sought stingless bees' nests, which he collected for his studies (more than 900 nests were studied in detail, among many observed). During these collections, he made notes in his travel diaries about where the nest was found and sketches of the landscape and related bioecological characteristics (aggressiveness, associations with other insects and microorganisms, number of nests found) and recorded images, which generated rich and extensive photographic material, recently digitized. In addition, when he returned to his laboratory at FFCLRP-USP, the data collected were consolidated in the illustrations made with a quill pen, some of which are presented here.

The Coleção Entomológica "Prof. J. M. F. Camargo" has been reorganized by the current curator, Prof. Eduardo A. B. Almeida, and its computerization was greatly aided by Dr. Fabio B. Quinteiro and Dr. Anne M. Costa. The scientific collaboration between

the Instituto Tecnológico Vale – Desenvolvimento Sustentável (ITV-DS) and the Coleção Entomológica “Prof. J. M. F. Camargo” enabled the retrieval of photographic material and the reorganization of the collection, a small part of which is presented here.

We are very interested in the bees of Pará, as the species that occur in the Serra dos Carajás have been intensively studied by the biodiversity team of the ITV-DS. However, for certified taxonomic identification of these bees, we needed reference material, which was carefully prepared by the collection curator; the specimens presented here are accompanied by the respective identification tags: who collected it and when, who identified it and the geographical origin of the specimens. Often, the specimens photographed are not from Pará but are within the area of occurrence of these species and were compared with the material from the nests deposited. The species of stingless bees selected for this collection were listed as occurring in the state of Pará (part of Eastern Amazon) in the review of the occurrence of bee species in Brazil.

Although the diversity of stingless bees in the Amazon is high, they have been little studied thus far. Therefore, recognizing the identity of forest species and their nests is not a trivial task. In his activities as a taxonomist and systematist, Camargo described three genera and 89 species of bees. In addition to this monumental work, he described the unusual habits of many of these species, which differed from the general pattern known up to that time for Brazilian social bees, for example, 1) *Ptilotrigona* and the storage of large amounts of dry pollen, through the association with the fungus *Candida* sp., and propolis in pots; 2) *Lestrimelitta* specialized in robbing resources stored in the nests of other species; 3) *Trichotrigona* sampled in the Amazon, with very small nests, without food pots, suggesting a pillage pattern different from that of *Lestrimelitta*; 4) obligatory necrophagous bees of the *Trigona hypogea* group; 5) *Schwarzula*, which obtain wax produced by the scale insects associated with their nests; 6) the minute bees and their habits of collecting salt and sweat; 7) *Duckeola ghiliani* defends its nests, and those close to their own, from the attack of the *Lestrimelitta* robbers; and many other examples that show us the diversity of behaviours and community of bees.

The work of Camargo with the Kayapó indians of Gorotire deserves special mention: he compiled, illustrated and recorded the knowledge of the great masters of bees (especially the shaman Kwyrà-Kà). These wiseman (*waianga*) deeply knew the bees and their products, which were much appreciated and had many biocultural meanings that were transmitted orally. Together with the anthropologist Darrell A. Posey, with Prof. Warwick E. Kerr and other distinguished researchers at the time, he helped to record the indigenous knowledge for future generations, having contributed to the development of an important glossary of technical terms for the bees in Kayapó, in English and Portuguese.

In this book, we compile the diversity of stingless bees in the state of Pará, showing the main characteristics of the Amazon vegetation in the initial chapter. The collected bees were deposited in the collection organized by the researcher at FFCLRP-USP, his institution, the Coleção Entomológica “Prof. J. M. F. Camargo”. To introduce the

biocultural approach to bees and their role in societies, we based ourselves on the indigenous knowledge of the Kayapó people. Next, we present the richness of the behavioural repertoire of some Amazonian stingless bee species, whose characteristics differ from the patterns common to other Meliponini species. Illustrations of bee nests that could be documented through photographs retrieved from Camargo's photo library, in addition to diagrams published by the researcher, are accompanied by geographic distribution maps obtained in the Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. The information presented here is important for the recognition of Amazonian species and for the biodiversity and maintenance of ecosystem services.

Vera Lucia Imperatriz-Fonseca



João Camargo during one of the Amazon expeditions

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Coleção Entomológica “Prof. J. M. F. Camargo”, a legacy of the scientist

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Biological collections are scientific depositories of key importance in the preservation and generation of knowledge about the diversity of living beings. Collections are one of the most essential sources of information supporting research on biodiversity, encompassing fields as diverse as taxonomy, ecology, biogeography, evolution, and genetics. This text addresses the Entomological Collection housed at the Biology Department, Faculdade de Filosofia, Ciências e Letras (FFCLRP) of Universidade de São Paulo, which was started between 1963 and 1965 by Professor João Maria Franco de Camargo (1941-2009). In 2011, this collection was officially named *Coleção Entomológica “Prof. J. M. F. Camargo”*, as a posthumous tribute to the researcher who greatly contributed to its establishment and growth for more than four decades.

The scientific trajectory of João Camargo was marked by scientific contributions of great importance for the description and understanding of the diversity of bees in the Neotropical Region, especially stingless bees (Apidae: Meliponini). His scientific production is reflected in more than 80 publications, which meant the construction of a magnificent framework of knowledge on the bee taxonomy, as well as their evolution and behavior (Pedro, 2009; Rasmussen, 2010). Throughout his career, Camargo built a research collection that initially consisted of a personal resource for his research needs, but that later became a scientific collection of global importance.

In the first decades of the development of what is currently represented by the Entomological Collection, the field expeditions carried out by João Camargo himself and his research team to various regions of Brazil (with a special interest in the Amazon) allowed the acquisition of material very relevant for the research on bees and other insects (Pedro, 2009). With its development, the collection also grew through the incorporation of material from research developed by students and collaborating researchers as well as by the exchange of specimens with other institutions. Currently, the Entomological Collection is rich in various groups of insects but is particularly

representative for bees, especially stingless bees. In this case, more than 80% of the Meliponini species of the Neotropical Region are accounted for, and a wide representation of the fauna of the Paleotropical and Indo-Australasian regions is also present.

The number of insects mounted on pins exceeds 250,000 specimens deposited at *Coleção Entomológica "Prof. J. M. F. Camargo"*, which is complemented by an extensive number of specimens preserved in liquid fixative. Type specimens (holotypes, paratypes, and paralectotypes) stand out – this material has a unique relevance in taxonomic research because they allow the names of the species to be safely associated with the biological entities represented by the species themselves.

The collection houses 3,832 type specimens of the order Hymenoptera and Diptera, of which 91 are holotypes and together represent 202 species of insects. Of these, the majority refers to names of Meliponini species (127 species), but it also includes species representing 6 other Apidae tribes and 9 other families of wasps and bees (Hymenoptera). The collection also houses an exceptional archive of 905 stingless bee nests, which includes works built by bees (pieces of nests) and more than 5,000 slides that depict aspects of the biology of these bees. The Entomological Collection began to be computerized in 2004, and currently, there is information (data and photographs) available for more than 100,000 specimens in the *speciesLink* (<http://www.splink.org.br>) and GBIF – Global Biodiversity Information Facility (Almeida, 2019) databases.

References

- Almeida EAB (2019) RPSP – Coleção Entomológica Prof. J.M.F. Camargo, FFCLRP/USP; v.1.12. Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo (USP). <https://doi.org/10.15468/fkx59c> (Accessed November 2019).
- Pedro SRM (2009) João M. F. Camargo – Um naturalista dedicado às abelhas (20.06.1941 – 07.09.2009). *Revista Brasileira de Entomologia* 53: 686-688.
- Rasmussen C (2010) João Maria Franco de Camargo (Anhembi, SP, 20 June 1941–Ribeirão Preto, SP, 7 September 2009). *Entomologia Americana* 116: 89–91.

Types of vegetation in the Amazon, with a focus on Pará

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Instituto Tecnológico Vale – Desenvolvimento Sustentável

Pará is the second largest Brazilian state, occupying an area of 1,248,000 km², between 2 degrees north and almost 10 degrees south of the equator. Pará, which is mostly composed of the Amazon biome, is on the northwest border of the Brazilian Cerrado (savanna), and currently, a total of 332 species of bryophytes (mosses and liverworts), 293 species of pteridophytes and lycophytes, 7 gymnosperms and 6,536 angiosperms have been recorded in its territory (FBO2020 in preparation).

Plant species most common in a given vegetation type are called dominant species, such as the açai palm (*Euterpe oleracea*), a very common palm on the riverbanks in all of Pará and dominant in the *várzea* (whitewater-flooded) forests and *igapó* (blackwater-flooded) forests. This concept of dominance may lead one to believe that the Amazon plant species are very common and occur throughout the biome, with a predominance of one hundred species widely distributed; however, in fact, there are many others that, at times, go unnoticed because they are less common or have a restricted distribution (ter Steege et al., 2013). A forest is defined as vegetation in which trees are the main component that most contributes to the biomass, and there may be one or more layers composed of different habits (shrubs, saplings) under a more or less continuous tree canopy. Due to the predominance of trees, the understory is shaded, and the herbaceous stratum is never continuous, as we see in grassland or open vegetation. To facilitate the understanding and consultation of this information, the text was subdivided into forest vegetation and grassland vegetation.

Types of forest vegetation

The forests of the state of Pará are very diverse and known locally as *igapó* forest, *várzea* forest, *terra firme* (unflooded) forest, liana forest and dry forest.

The presence of different forest types is determined by the soil type, with different characteristics, such as humidity, altitude, slope, pH, permeability, degree of flooding, etc.

To recognize the different forest types, we considered the height, density, number of layers within the forest, number of lianas or climbers, presence of palm trees, density of the understory, and geographic and geological characteristics of the site, such as presence of rivers, type of water, frequency of flooding, substrate and slope. Some species or genera that are more frequent and considered dominant for each type of forest vegetation are also taken into account.

Dense ombrophilous forest (*terra firme* forest)

Generally located in flat sites, with little slope, and away from the influence of rivers, these are the highest forests in the Amazon. In them, the tallest trees form a cover called a canopy, with the treetops between 25 and 35 m in height. Some taller trees rise above this canopy, called emergent trees, with branches and canopy extending

approximately 10 m above the rest, among which we commonly found Brazil nut (*Bertholletia excelsa*), *quaruba* (*Vochysia maxima*), *quarubarana* (*Erisma uncinatum*), manbarklak (*Eschweilera* spp.), *tauari* (*Couratari* spp.) and *fava-arara-tucupi* (*Parkia multijuga*).

Dense ombrophilous forest in Carajás, PA (photo: J.M. Rosa)



In the forks of large trees, especially those with thick bark and horizontal branches, one can find epiphytes, which are brought by wind or by animals, such as orchids and bromeliads, or hemiepiphytes. These germinate in the soil and begin their life cycle as vines and later adopt an epiphytic habit, as in the case of Araceae, which often reach large size, with aerial roots hanging towards the forest soil.

Under the canopy, it is possible to observe shrubs and saplings up to 10 m in height, which will not reach the light and thus live permanently in the shade. Additionally, herbaceous plants and dark-leaved ferns adapted to extremely low luminosity and very high humidity also occur.

In the soil, in between and on the roots of the trees, we see a large accumulation of dry leaves, wood stumps, fungi, petals and fruits, which together form a layer called litterfall, but usually, there is no water accumulated in puddles. In the middle of the litterfall, we can find small herbs with varied colours, such as white, yellow, pink and red, some parasitizing roots, such as *Helosis cayennensis* and *Langsdorffia hypogaea*, and some decomposers, such as *Voyria* species. It is this moist layer of leaves that protects a hidden universe, where the roots develop and breathe and establish associations with various microorganisms that are responsible for nutrient cycling.

Open ombrophilous forest (liana forest)

In the Southeast and Southern regions of Pará, where the Amazon biome borders the Cerrado (Veloso et al., 1991), the forest is more open than the dense ombrophilous forest. Known as open ombrophilous forest with lianas, it is popularly known as liana forest. This type of forest occupies both flat sites and hillsides. Its characteristics include a discontinuous canopy, formed by scattered trees, ranging between 15 and 25 m in height, and emergent trees generally shorter than what we find in dense forests. In this environment, it is very common to find woody vines (also known as lianas) interspersed along the paths, making this type of forest one of the most difficult environments to penetrate. These vines use the support of the trees to reach the sunlight, growing, blooming and fruiting above the tree canopy, and possess winged fruits and seeds that hover over the forest and are dispersed by the wind. *Escadas-de-jabutí* (*Schnella* spp.) and other woody lianas, also known as vines, can be seen from the ground, with their twisted branches rise until getting lost in the canopy. The density of vines is one of the factors that makes the trees weaker, causing canopy obliteration and falling branches that, in turn, leads to these forests not reaching the same height as the dense ombrophilous forest. Some of the most common trees are pequi (*Caryocar villosum*), cacauí (*Theobroma speciosum*), and sterculias (*Sterculia* spp.) – which are relatives of cocoa and cotton – in addition to several Fabaceae, such as *paricá* (*Schizolobium parahyba* var. *amazonicum*) and *caneleiro* (*Cenostigma tocantinum*), with tortuous and hollow trunks. Also notable is the presence of several palm trees, such as babassu palm (*Attalea speciosa*), urucuri palm (*Attalea phalerata*), *bacaba-de-leque* (*Oenocarpus distichus*) and tucuma (*Astrocaryum aculeatum*), used



Open ombrophilous forest surrounding the Laguna da Mata Trail, Carajás National Forest, PA (photo: J.M. Rosa)

as food by fauna and by the local human population in different ways.

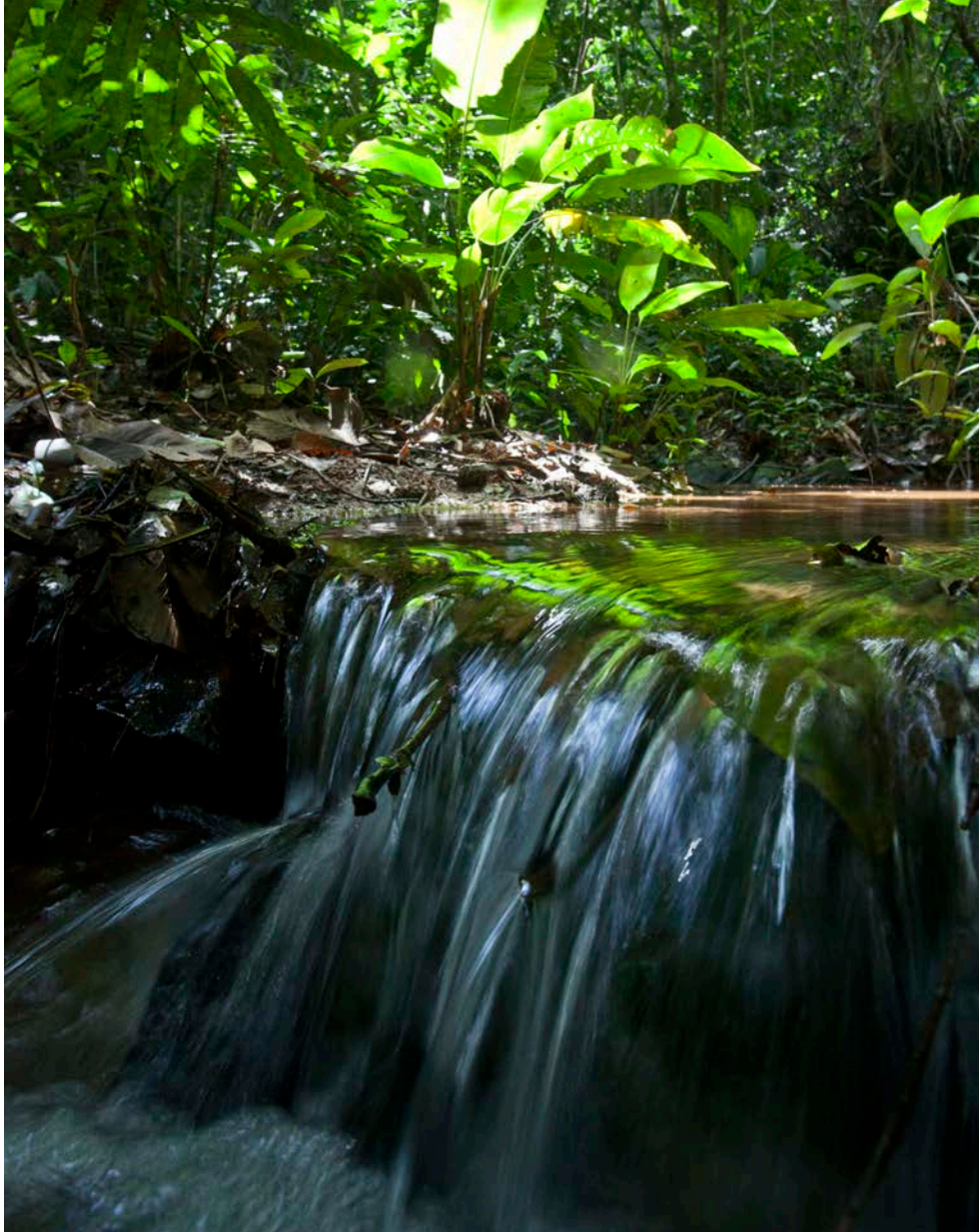
During the rainy season, the winds can break branches or even the emerging part of trees weakened by strangling vines and termites and even by the weight of large climbing vines, such as cat's claw (*Uncaria guianensis*), whose curved spines get hooked in the vegetation, while monkey orange (*Strychnos* spp.) and tayuya (*Cayaponia tayuya*) have simple or more complex tendrils that attach to the branches of other plants. The old branches of the *escada-de-jabutí* (*Schnella* spp.) form true zigzagging stairs, which seem to disappear into the canopy. The forest soil is shallow and offers little support for the roots, with frequent falling of entire trees.



Semideciduous forest in Harpia Stone, Carajás National Forest, PA (photo: J.M. Rosa)

Semideciduous forest (dry forest)

On rocky soils and in more exposed areas or with greater slope, especially on granite or even sandy substrate, we can observe another type of vegetation, the dry forest, or semideciduous forest (Veloso et al., 1991). In these locations, the water does not remain in the soil for a long time, draining immediately after the rainy season. Reaching 10 to 15 m in height and forming a more or less continuous canopy, the trees and shrubs that grow in these locations are more resistant to drought, and many of them lose their leaves during the dry season, hence the name 'semideciduous'. In this habitat, there is a predominance of plants with thorny branches and trunks with thorns and other curious excrescences in the bark, in addition to a large number of lianas. *Mamica-de-porca* (*Zanthoxylum rhoifolium*), *mulungu* (*Erythrina ulei*), *monjoleiro* (*Senegalia polyphylla*), *jaborandi* (*Pilocarpus* spp.), *carapança-vermelha* (*Coutarea hexandra*), *glassywood* (*Astronium graveolens*), *imbiuruçu* (*Pseudobombax longiflorum*) and *ipe* (*Handroanthus* spp.) are common woody species in this habitat type. In the soil, the litterfall layer is dense, and in places where the tree cover is thinner and there is greater penetration of light, terrestrial bromeliads and other plants with thorns grow, making it difficult to penetrate. Semideciduous forests are often associated with rocky outcrops, with some cacti, orchids and rupicolous begonias.



Igapó forest in Carajás National Forest, PA (photo: J.M. Rosa)

***Igapó* forest**

In the area of influence of the drainage of the Amazon river's clear water, known as clearwater or blackwater rivers, we find the *igapó* forests. These habitats are influenced by the movement of waters that temporarily flood the forest and occupy a narrow strip between the river margins and *terra firme* forest. There are some species of plants able to grow in these locations that are submerged for months, remaining inactive for part of the year. The waters rise up to 5 or more metres in height, flooding much of the forest during the flood season and dropping again during the ebb period. These periodic floods are influenced by rains that occur at the headwaters of tributaries many kilometres away and not necessarily due to local rainfall. Occasionally, some trees reach at least 30 m in height, such as kapok (*Ceiba pentandra*), interspersed by a dense canopy.

The tolerance capacity of flooded forest species, whose trunks remain under water for months during the rainy season, is impressive. The walking palm or cashapona

(*Socratea exorrhiza*), adapted to grow in flooded soil, has stilt roots that contribute to its fixation. Other species, such as manpara renaco (*Macrolobium acaciifolium*) and *ingazeiro* (*Inga flagelliformis*), are common on the edge of the igapó forest, along with several species of strawberry guava and little guava that knock fruits into the water that are then consumed by pacu fish and other frugivorous fish. The *pente-de-macaco* (*Apeiba tibourbou*) is a tree with strange, light and hairy fruits, which float in the river currents, using water to disperse its seeds. The general aspect of this vegetation is fascinating, with semi-submerged trunks and branches and trees with stilt roots of varied morphologies reflected on the calm surface of rivers.

Várzea forest

In the vicinity of large rivers of turbid water, known as whitewater rivers, there are backwater areas flooded and constantly fertilized by the water flow that rises during the rainy season and drops during the dry season. In these locations, the *várzea* forest, or flooded ombrophilous forest, is established (Veloso et al., 1991). In the *várzea* forest, the canopy is discontinuous and difficult to distinguish.

Várzea forest in Carajás
National Forest, PA
(photo: J.M. Rosa)

Species such as andiroba (*Carapa guianensis*), kapok (*Ceiba pentandra*), and several palms, in addition to the so popular açai (*Euterpe oleracea*) and buriti or miriti (*Mauritia flexuosa*), also occur in flooded areas. Other palms, such as



moretillo palm (*Mauritiella armata*) and ubussu (*Manicaria saccifera*), also grow in the floodplains of these rivers.

Many types of aquatic plants occur in floodplains: free floating plants and floating-leaved plants attached to the soil of the lagoons and that depend on buoy-like structures for flotation (Zappi, 2017). Other plants are totally or partially submerged and are usually fixed to the substrate in the margins of rivers and lakes. Emergent plants, where only the base and roots remain permanently or even temporarily under water, form large populations on the riverbanks. Those include Amazon water lily (*Victoria amazonica*), the region's iconic plant, and *aninga* (*Montrichardia linifera*), with large populations.

Types of grassland vegetation

Amazonian savanna and *campinaranas*

Locations generally associated with sandbanks formed by rivers or with sandstone or even granite rocky outcrops, where the soil is poor and shallow and often temporarily flooded, favour the establishment of different physiognomies of open and grassland vegetation known as *campinarana* (low open forests on white-sand savannas),

Amazonian savanna in the Itauajuri Mountains, Monte Alegre, PA (photo: D.C. Zappi)

Amazonian savanna (found at a certain altitude and distant from the most expressive waterways) and Amazonian rocky fields (on rocky outcrops) (Pires and Prance, 1985). In these locations, we observed similar physiognomies to those found in the Cerrado biome. Even some widely distributed





Campinarana in
the Ariramba
Fields, Óbidos, PA
(photo: D.C. Zappi)

species associated with the Cerrado, such as the sandpaper tree (*Curatella americana*), *bananeira* (*Salvertia convallariodora*), *carne-de-vaca* (*Roupala montana*) and several mirixis (*Byrsonima* spp.) may be found in these types of vegetation. One of the dominant species is tauroniro (*Humiria balsamifera*), which may be present in many environments, ranging from subshrubby to arboreal habit. Regarding the herbaceous stratum, it is more or less continuous and includes several Poaceae, Cyperaceae, Eriocaulaceae and Xyridaceae in more marshy areas and subshrubs and shrubs of the families Melastomataceae and Myrtaceae but also *marmelinho* (*Licania incana*).

The *campinaranas* are open environments, with no tree specimens, that occur in sedimentary plains formed by river courses. The presence of flat rocks at shallow depths underneath the sandy substrate causes these habitats to have a significant herbaceous stratum, and the shrubs and subshrubs that occur there have superficial roots. Sometimes, temporary lakes or marshy soils form, favouring the presence of aquatic plants.

The savanna physiognomy is found in deeper soils that are also sandy and poor, with or without the presence of rocky outcrops. Another physiognomy found is rocky fields on rocky outcrops, as seen in Monte Alegre and Alter do Chão, in the middle

Amazon region. The specific compositions of *campinaranas*, Amazonian rocky fields and Amazonian savannas in the same site are very similar. On the other hand, there is much variability from one site to another due to the isolation of these open environments within a forest matrix.

The relationship between the Amazonian savannas and the Cerrado biome is tenuous (Ratter et al., 2003), and the isolation dates back to before the Quaternary (Buzatti et al., 2017; Resende-Moreira et al., 2019).

Rocky fields on *canga*

In the Carajás region, usually above 600 m altitude, the iron ore-rich lateritic crusts, known as *canga* (ironstone outcrops), contain a specific type of rocky field (Viana et al., 2016; Mota et al., 2018; Zappi et al., 2019), researchers at the Museu Paraense Emílio Goeldi (MPEG). At approximately 6 degrees south of the equator and surrounded by open ombrophilous forest, the *canga* outcrops provide an inhospitable, rocky, open environment where the generally open and sparse vegetation is deciduous during the dry season and very exuberant due to the annual herbs that develop during and after the torrential rains that fall between November and May (Zappi, 2017). The *canga* substrate may be more or less compacted, which, together with different altitudes and drainage, allows the development of microhabitats, such as lakes, marshy fields, grasslands, shrubs and bushes, with many species of endemic plants. There are also caves formed by recesses of the lateritic crust, especially at the boundaries between the *canga* and the forest around it.

Most of the plants reach less than 2 m in height, and the soil is often exposed or covered by a dense grassy-woody layer with annual subshrubs and herbs. Between 1 and 3 m, shrubs and saplings appear isolated or in small groups on the landscape. The most common species are *vassourinha* (*Callisthene microphylla*), *canela-de-ema* (*Vellozia glauca*) and *murici* (*Byrsonima chrysophylla*), associated with the climbing shrub known as red hot poker vine (*Norantea guianensis*), *pata-de-vaca-miúda* (*Bauhinia pulchella*) and *erva-cidreira-da-canga* (*Lippia grata*). We can observe among these species the predominance of small and hard leaves, some hairy, many of them positioned vertically relative to the soil, a strategy that minimizes the direct effect of strong sunlight. The structure of small leaves may also be related to greater resistance to dehydration than thinner and expanded leaves, which are common in forest environments.

On the shrubs, we see vines, such as *flor-de-carajás* (*Ipomoea cavalcantei*), with attractive red flowers pollinated by hummingbirds. Other climbing plants belonging to the *mangaba* family (*Mandevilla scabra*, *Blepharodon pictum*) are pollinated by butterflies and bees. In the wettest and rocky parts, populations of *cara-de-cavalo* (*Philodendron wullschaegelii*) and bamboo-orchids (*Sobralia liliastrum*) can be found; on exposed rocks, we find lady of the night cactus (*Cereus hexagonus*) and *gravatá-da-canga* (*Dyckia duckei*). During the rainy season, *canga lajedos* (flat rocky surfaces where the bedrock is exposed) give rise to marshes and temporary lagoons that house large populations of endemic

species, such as *boca-de-leão-da-canga* (*Utricularia physoceras*), *Perama carajensis* and *Brasilianthus carajasensis*, in addition to *sempre-vivas* (*Paepalanthus fasciculatus* and *Xyris brachyphylla*) and species of *Polygala*, *Sauvagesia* and *Burmannia* amid a high abundance and diversity of Poaceae and Cyperaceae. The high rainfall alternating with the dry season, the wind and even lichens, mosses and roots of plants that germinate and grow in the crevices of the rocks cause weathering and the formation of a thin layer of soil. Dried leaves and other plant residues accumulate in the area and, on this mixture of organic and inorganic deposits, grow mats of Poaceae (*Paspalum spissum*, *Trachypogon spicatus* and *Mesosetum* sp.) Cyperaceae (*Rhynchospora globosa*), which reach between 50 and 80 cm in height and are interspersed with shrubs.

The *canga* is a dense and partly impenetrable substrate, and the water forms puddles on its surface or accumulates and runs according to the slope of the terrain. Small watercourses are formed in larger crevices, converging into waterfalls that become dry between the months of May and September and active again in the rainy season. The rapid life cycle of annual *canga* species is a strategy to survive in habitats with a marked dry season. The seeds of these plants germinate as soon as the first rains fall between October and November. Foliage develops rapidly, and flowering begins in April. During the months of August to October, there is no sign of the presence of these species in the region.

Rocky field on the
canga in Carajás
National Forest, PA
(photo: J.M. Rosa)



Recent studies have outlined the importance of vegetation on *canga* as a resource for bees that inhabit the surrounding forests (Guimarães et al., in press), recording the path of the pollinator between habitats during the flowering peaks of species that occur in the *canga*.

Amazon restinga

The coastal region of Pará includes large sandy areas formed by the Amazon River estuary, where dunes, lakes and *veredas* (palm swamps) of lush vegetation are established. Known as restinga (sandy coastal plains), these coastal formations are extremely heterogeneous and can be represented by a gradient ranging from coastal dunes to forests with canopies in the Atlantic Forest biome. On the Amazonian coast, they comprise mangroves, dense scrub or *veredas* and periodically flooded coastal fields (Amaral et al., 2008).

Restinga of Princesa beach, Algodual, PA
(photo: D.C. Zappi)

The most common species in the dense-scrub-type restinga include bushes dominated by perennial shrub species such as cocoplum (*Chrysobalanus icaco*), cashew tree (*Anacardium*



occidentale), *olho-de-pomba* (*Pagamea guianensis*) and limber caper (*Cynophalla flexuosa*), in addition to tauroniro (*Humiria balsamifera*), which are also common in the Amazon savannas and *campinaranas*. In the most inland area, it is common to observe populations of bacuri (*Platonia insignis*). In permanently flooded areas, we find buriti or miriti (*Mauritia flexuosa*) and moretillo palm (*Mauritiella armata*), accompanied by annual herbaceous plants of the families Cyperaceae, Xyridaceae and Eriocaulaceae, which are more predominant during the rainy season.

Anthropogenic influence on vegetation

Currently, we know that even before the arrival of the Europeans to the Amazon, the indigenous tribes that populated the region had knowledge about the management of local flora and fauna (Posey, 1985; Balée, 1993), creating environments similar to vegetable gardens and transporting seeds and plant seedlings from one location to another. Evidence of soil management that includes a partial process of felling and burning (*coivara*) combined with recycling of ceramic fragments and food waste, forming the so-called Indian black earth (*terra preta de índio* – TPI), are common in the Amazon territory. In these areas, there is an accumulation of useful species for humans, such as Brazil nut (*Bertholletia excelsa*), cupui (*Theobroma subincanum*), *pequia* (*Caryocar villosum*), passion flowers (*Passiflora* spp.), cassava (*Manihot esculenta*) and maize (*Zea mays*), suggesting the existence of an agroforestry system developed over thousands of years in the Amazon territory (Clement et al., 2015; Levis et al., 2018).

In northeastern Pará, the Bragantina region was home to the first experiences of deforestation for food farming, which mostly followed European agricultural practices, without taking into account the equatorial climate or the methods used by the Amerindians. Much of the destruction of forests in the region dates back to the period of the rubber boom in the Amazon (1873 to 1912) and the growth in demand for food products within this biome.

Conversely, southwestern Pará and northern Mato Grosso were the scenes of a more recent expansion, which started with the inauguration of the Belém-Brasília highway in 1959, expanding deforestation with the relocation of loggers from the southern states of the country to the region and, later, with the formation of pastures and the development of extensive livestock production. This region is known as the arc of deforestation, where deforestation and the management procedures adopted, including burning and sowing of exotic grasses, dramatically modified the forest vegetation. This region is considered of great vulnerability for the advancement of deforestation in the Amazon (Zappi et al., 2016).

A system more compatible with the preservation of the Amazon physiognomy and the maintenance of carbon sequestration performed in this biome are agroforestry systems (Nunes et al., 2017), including the concept of polyculture, which involves several species dividing the same space (opposite to monocultures), the presence

of productive trees shading and protecting the soil, the use of natural recycling of leaves and branches in the forest soil and the seeding of seed mixes (*muvuca de sementes*). These systems evoke the land use practices of the Amazonian tribes in pre-Columbian times, pointing to new possibilities based on ancestral experiences. It is worth remembering that unlike what was previously thought, there was a period in which the Amazon accommodated large human populations in its forests (Palace et al., 2017).

References

- Amaral DD, Prost MT, Bastos MNC, et al. (2008) Restingas do litoral amazônico, estados do Pará e Amapá, Brasil. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 3: 35-67.
- Balée W (1993) Indigenous transformation of Amazonian Forests: An example from Maranhão, Brazil. *Homme* 33: 231-254.
- Buzatti RS de O, Lemos-Filho JP, Bueno ML, Lovato MB (2017) Multiple Pleistocene refugia in the Brazilian cerrado: evidence from phylogeography and climatic niche modelling of two *Qualea* species (Vochysiaceae). *Botanical Journal of the Linnean Society* 185: 307-320.
- Clement CR, Denevan WM, Heckenberger MJ, et al. (2015) The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B* 282: 20150813.
- FBO2020 (em preparação) Flora do Brasil online 2020, Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/reflora/listaBrasil/ConsultaPublicaUC/ResultadoDaConsultaNovaConsulta.do#CondicaoTaxonCP> (Accessed March 2018).
- Guimarães JTF, Costa L, Batista Jr WF, et al. (in press) Melissopalynology reveals the foraging preferences of the stingless bee *Melipona seminigra pernigra* Moure & Kerr 1950 (Apidae: Meliponini) in Cangas of Serra dos Carajás, Southeastern Amazonia. Preprints 2019: 2019100134.
- Levis C, Flores BM, Moreira PA, et al. (2018) How people domesticated Amazonian Forests. *Frontiers in Ecology and Evolution* 5: 171.
- Mota NFO, Watanabe MTC, Zappi DC, et al. (2018) Amazon canga: the unique vegetation of Carajás revealed by the list of seed plants. *Rodriguésia* 69: 1435-1487.
- Nunes S, Gatti G, Diederichsen A, et al. (2017) Oportunidades para Restauração Florestal no Estado do Pará. Belém: Imazon.
- Palace MW, McMichael CNH, Braswell BH, et al. (2017) Ancient Amazonian populations left lasting impacts on forest structure. *Ecosphere* 8: e02035.
- Pires JM, Prance GT (1985) The vegetation types of the Brazilian Amazon. In: Prance, G.T. & Lovejoy, TE (eds.) *Amazonia: Key Environments*. New York: Pergamon Press, pp. 109-145.
- Posey DA (1985) Indigenous management of tropical forest ecosystems: the case of the Kayapó indians of the Brazilian Amazon. *Agroforestry Systems* 3: 139-158.
- Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: Comparison of the woody vegetation of 376 areas. *Edinburgh Journal of Botany* 60: 57-109.
- Resende-Moreira LC, Knowles LL, Thomaz AT, et al. (2019) Evolving in isolation: Genetic tests reject recent connections of Amazonian savannas with the central Cerrado. *Journal of Biogeography* 46: 196-211.

- ter Steege H, Pitman NCA, Sabatier D, et al. (2013) Hyperdominance in the Amazonian tree flora. *Science* 342:1243092.
- Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE, Rio de Janeiro.
- Viana PL, Mota NF de O, Gil A dos SB, et al. (2016) Flora of the cangas of the Serra dos Carajás, Pará, Brazil: history, study area and methodology. *Rodriguésia* 67:1107-1124.
- Zappi DC (2017) Paisagens e Plantas de Carajás/Landscapes and Plants of Carajás. Belém: Instituto Tecnológico Vale.
- Zappi DC, Milliken W, Lopes CRAS, et al. (2016) Xingu State Park vascular plant survey: filling the gaps. *Brazilian Journal of Botany* 39: 751-778.
- Zappi DC, Moro MF, Walker B, et al. (2019) Plotting a future for Amazonian canga vegetation in a campo rupestre context. *PLoS ONE* 14:e0219753.

Indigenous knowledge of the Kayapó people regarding stingless bees

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Introduction

The Kayapó people were intensively studied by the anthropologist Darrell A. Posey and his collaborators between 1970 and 1990. Knowledge about cosmology, the environment, and cultural traditions, that had previously only been transmitted orally, was for the first time, documented and disseminated, based on the traditional knowledge of the Gorotire Village indigenous community in Pará. Their focus on agriculture and forest resource management (for example, Kerr and Posey, 1984; Posey, 1985) has been emphasized in several previously published reviews on this subject. However, the study of bees, their products and their use by indigenous people (Posey 1983; Posey and Camargo, 1985; Camargo and Posey, 1990) deserves further attention due to the wealth of local knowledge on these insects found among members of the Gorotire Village community, and to ensure this knowledge is accurately transcribed and recorded in scientific collections and publications for diverse future audiences.

In rereading these works, my main aim was to understand how indigenous people, who lived in such diverse Amazon forest habitats, perceived bees, how they used bee products, and what they knew about bee biology and management. Bees, as well as wasps and other social insects, are part of their cosmology and serve as an example of social organization in the villages. The Kayapó people knew 56 species of stingless bees and semi-domesticated 9 of them for the collection of honey and other products. They ate the pollen and larvae stored in bees' nests and used other bee products as medicines. In addition, cerumen, which is used for different purposes by indigenous people of many ethnic groups in the Americas (Quezada-Euán et al., 2018; Hill et al., 2019), was traded as raw material for the production of headdresses, bows and arrows, and to waterproof baskets. For the Kayapós, cerumen had greater meaning, because it

was used to make a traditional helmet (the *mê-kutôm*) used during shamanic rituals in which young men receive their adult name. This is a significant ancestral rite in social organization, uniting the past and present of Kayapó life.

Among the Kayapó people of Gorotire Village, there were experts who had a vast knowledge of bee nesting habits, biology, use of bee products in daily life and links with cosmology. The specific vocabulary used to name the body parts of bees and nests, exemplified in the illustrations of this chapter, demonstrates the in-depth knowledge of these experts, which had been passed on only through oral teachings until it was documented by Posey and collaborators and in other publications. Since the beginning of research on the bees used by the Kayapó people, Camargo followed with interest the development of the field of ethnobiology, identified the bees collected by Posey, and participated in a trip to the village, where he lived alongside these local experts of bees. This is one of the richest parts of his research, dealing with the relations between indigenous peoples and natural resources, comparing his observations with the scientific knowledge of the time and establishing deep ties of respect for the masters Kwyrà-Kà (who communicated in Portuguese), Irã and Krã.

João Camargo was also an artist and, using his sketches, wrote down the names given to the different structures of nests, body parts, stages of development, behaviour, and names of bees, among others. Thus, a glossary with these Kayapó names was created and translated into Portuguese and English. The drawings presented here were authored by him and were graciously shared for reproduction by the Annals of Carnegie Museum, where they were first published by Posey and Camargo (1985). Subsequently, with additional notes in Portuguese, this work was published in the Boletim do Museu Paraense Emílio Goeldi. The annotations presented here were transcribed by Posey (1983), Posey and Camargo (1985) and Camargo and Posey (1990).

Bees and cosmology

Cerumen, the primary building material of stingless bee nests, consists of wax produced by bees mixed with plant resins collected from the surrounding habitats. However, for the Kayapó, it has a direct connection with cosmology. They believed that their ancestors lived in the sky and descended to earth by a cotton rope, which landed in the burrow of an armadillo, a much-sought after game species. Their ancestors also brought with them a ball of cerumen, with which they made the hat, *mê-kutôm*, to fit the head of a young man receiving his full name. This cerumen ball is buried in the floor of the family home and reused in other rituals. The *mê-kutôm* (Fig. 1), described below (Posey, 1983), has a special symbolic role because it is the link between the Kayapó of today and their ancestors:

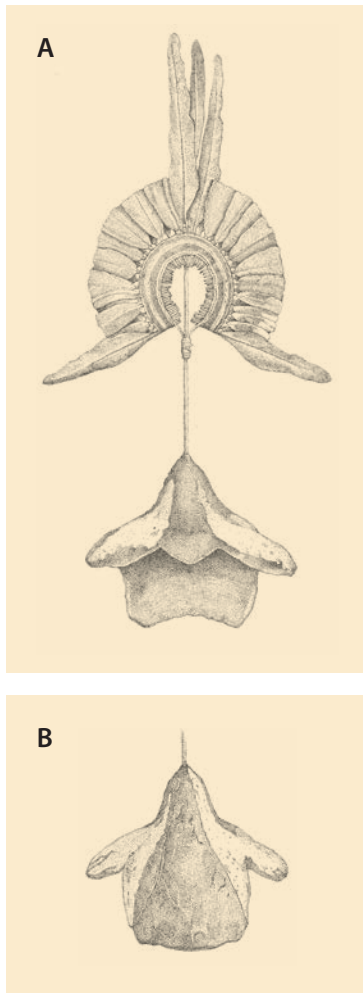


Fig. 1. Photograph reproduction of the *mē-kutôm*. Based on Campos (2006). (art: J. Silveira)

delivered to the wives or to the oldest woman in the house, who distribute it among the family members. The hunting of bee nests in the search for honey and cerumen is also a male activity performed in Gorotire Village, mainly by shamans. They are not afraid of the spirits and search for the nests at night, guided by the bee fanning noise, which they can distinguish for each species. They mentally mark where the nests are and return during the day to harvest the honey, which rarely makes it to the village. It is consumed where it is collected and in a very peculiar way. Using several banana leaves, they make a container where honey is stored. They chew the stalk base of wild ginger, which becomes spongy and is used as a spoon, which is dipped in the honey and shared that way. The brood combs and pollen contained in the pots are also considered a delicacy and eaten *in situ* by the hunting party. Sometimes honey,

"The mē-kutôm has a very symbolic shape. The front points to the east (where the sun rises, kaikwa kratx); the back points to the west (sunset, kaikwa-not). It includes 2 "legs" (pa) that correspond with the cardinal directions, pointing north and south. Areas that represent the geographic relationships between the village (nipok) and the fields are painted on these "legs". The central circle, slightly elevated, represents the village but also represents the sun. Within the nipok, there is another small circle that represents the moon superimposed on the sun. From the cardinal points emerge small representations that indicate the path of the sun and the moon through the sky (kaikwa) and over the earth (pyka):

The small circle (nipok) seen from above is an elevation where a rod is fixed, over which a bamboo and cotton arch are woven. Macaw feathers are inserted in the bamboo to produce an arch of red and blue feathers, which represent the sky (kaikwa)".

Other cosmological aspects of the Kayapó people were reviewed by Campos (2006). He also emphasized the importance of observing celestial movements by the Kayapó to guide the beginning and end of the fishing, hunting, and planting seasons, among others.

Hunting and honey

Male and female activities in Kayapó villages are pre-established socially. During hunting, which is carried out by men, the captured animal is



Fig. 2. A. Kwyrà-Kà collecting honey from a stingless bee nest. **B.** Kwyrà-Kà and honey stored in a container made of leaves, ready for transport. (photo: J. M. F. Camargo; Coleção Entomológica “Prof. J. M. F. Camargo”)

found the nest, the ecological zone, the tree, and the name of the bee, and the nest becomes his property. When the tree is tall, a small support platform is prepared with sticks and branches tied with lianas, so that the man can use an axe (Camargo and Posey, 1990) (Fig. 3).

When the honey and the offspring are removed from a nest, one part is left in the tree hollow for Bep-kororoti, who is a powerful shaman that was carried to the sky by a ray of light. Therefore, Bep-kororoti lives in the clouds, from where he sends rain, thunder, and lightning. Bep-kororoti likes honey, which encourages the indigenous to leave for him part of the nest, brood combs and food pots. Thus, the colony is re-established and can be reused the following year.

The worship of Bep-kororoti has ensured that populations of stingless bees near hunting areas have remained high over many years. The wax is also related to Bep-kororoti. When burned, it produces a cloud of smoke that wards off evil spirits, purges the houses of the ancestral spirits who did not leave and protects the children from witchcraft. Its use in the manufacture of artifacts is also common – bows and arrows are made with cerumen as the means to attach feathers, and the resin (*breu*) of plants

which may be partly fermented causes drunkenness (Posey, 1981). Any man who finds a tree with a nest, especially if it is in the capoeira (secondary forests) of his family, has the right to enjoy it: he warns his companions exactly where he

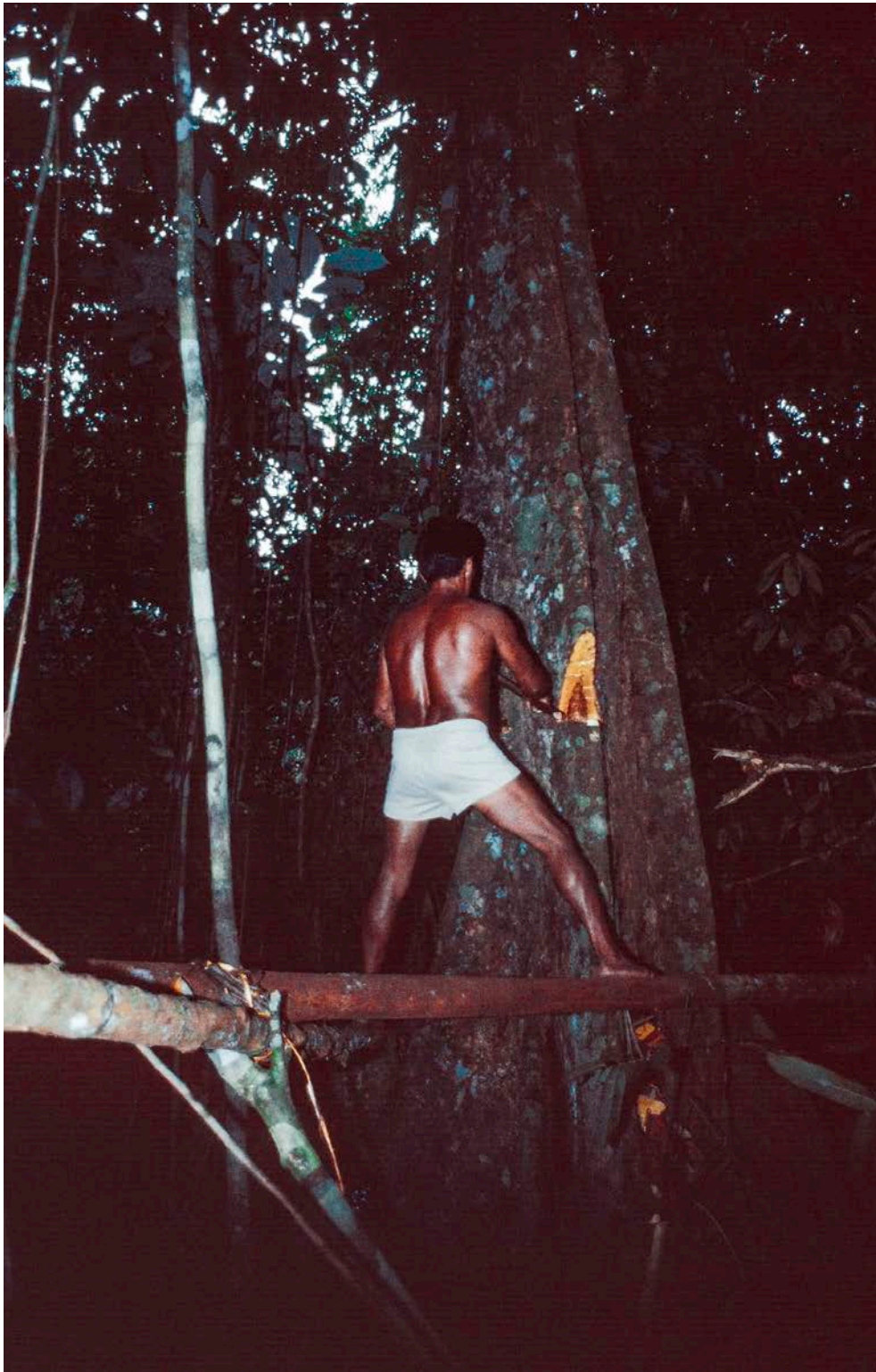


Fig. 3. The collection of products from a *Melipona paraensis* nest. (photo: J. M. F. Camargo; Coleção Entomológica "Prof. J. M. F. Camargo")



Fig. 4. *Apis mellifera* in Gorotire, PA. (photo: J. M. F. Camargo; Coleção Entomológica "Prof. J. M. F. Camargo")

collected by bees and deposited in nests is used to make the bow more malleable and robust.

The management of bees

Several bee species are known to men and women in the village and are usually associated with nests. Among these, some are widely known, such as *Melipona flavolineata*, *Trigona dallatorreana* and *Apis mellifera*. Reports of the arrival of Africanized bees (*Apis mellifera scutellata*, Fig. 4) in the village during the full moon of February 1966 are noteworthy. They are known for their defensiveness, for their high production of very sweet honey, and for having greatly decreased the availability of honey from other species of stingless bees. Camargo and Posey (1990) reported that the defensiveness of *Apis* decreased with time and that these bees were considered the strongest, replacing other species. In the classification of bees by their defensive behaviour, Africanized bees were considered very aggressive, and they sting; therefore, other management methods were necessary for this species. Shavings of the toxic vine *Tanaecium nocturnum* was placed in small quantities at the entrance of aggressive colonies, and the bees either fall asleep or die. Camargo and Posey (1990) reported that this vine was placed for a short period of time in the entrance of a *M. flavolineata* nest and, within 1.5 min, the bees began to die.

The Kayapó people recognize species of stingless bees whose nests can be explored periodically, either by harvests in successive years (a) or by bringing the nests near their houses (b) – *Melipona fasciculata* (a), *M. flavolineata* (a, b), *M. seminigra* (a, b), *Trigona amalthea* (a, b), *T. dallatorreana* (a, b), *Trigona cilipes*, *T. pellucida*, *Scaura longula*, and *Frieseomelitta* sp. (a). *Apis mellifera* is also managed every year for the collection of honey, which has commercial value; however, many among the community prefer the taste of stingless bee honey. *Melipona flavolineata* (*ngài-kumrex*) is a notable species because its wax can be used to manufacture *mê-kutôm* and the honey is greatly appreciated.

Stingless bee nests

For each vegetation type, the indigenous experts know which species of bees can be found and where they nest. The nests are grouped into basic categories identified by the Kayapó people and were described by Camargo and Posey (1990) (Fig. 5) – the wide diversity of nesting habits of stingless bee species is presented in the collection of stingless species and their nests. The entrances of nests also vary according to each species, such that they are important for identification and, therefore, also have special names (Fig. 6). The shape, texture, colour and smell of the entrance, in addition to the material used in its construction (clay, resin, cerumen, plant particles), are considered for bee identification.

Internal architecture of nests and food

The nests of stingless bees have a basic shared organization, such as a *Melipona* sp. nest occupying a pre-existing tree hollow (Fig. 7). All parts of the nest have Kayapó names, which is well explained by Camargo and Posey (1990). They recognize that pollen (*A-ũ*) is collected in flowers and transported to the nest, where it is placed in pots (*nhumê*). They also describe that the pollen taken to the nest is mixed with water droplets from the bee's mouth to form *nhum*, which is then fermented and semi-liquid pollen in some species. *Nhum* is the food of larvae. They also mention that the royal cells (the offspring of the queen bees) are fed a mixture of *nhum* and *mehn-kangô* (honey and pollen, respectively).

Camargo also describes how honey (*mehn-kangô*) is formed, according to the accurate observations of the community experts. It comes from the water of flowers (nectar, *pidjôrã-kangô*), collected and transported by bees and stored in pots (*mehn-ê-krê*). The nectar of different flowers has different densities and flavours, and the mixture results in honey with good quality and flavour (*mehn-kangô-abenkôt*). When the mixture is complete (*arup-metx*), the pots (*nhiên-djà*) are closed with wax (*ãn-je*). Brood cells are individually constructed to form clusters, as in *Frieseomelitta*, or stacked horizontal combs, as in most genera of stingless bees. When brood cell construction is complete, the queen and some workers gather in a characteristic ritual for each

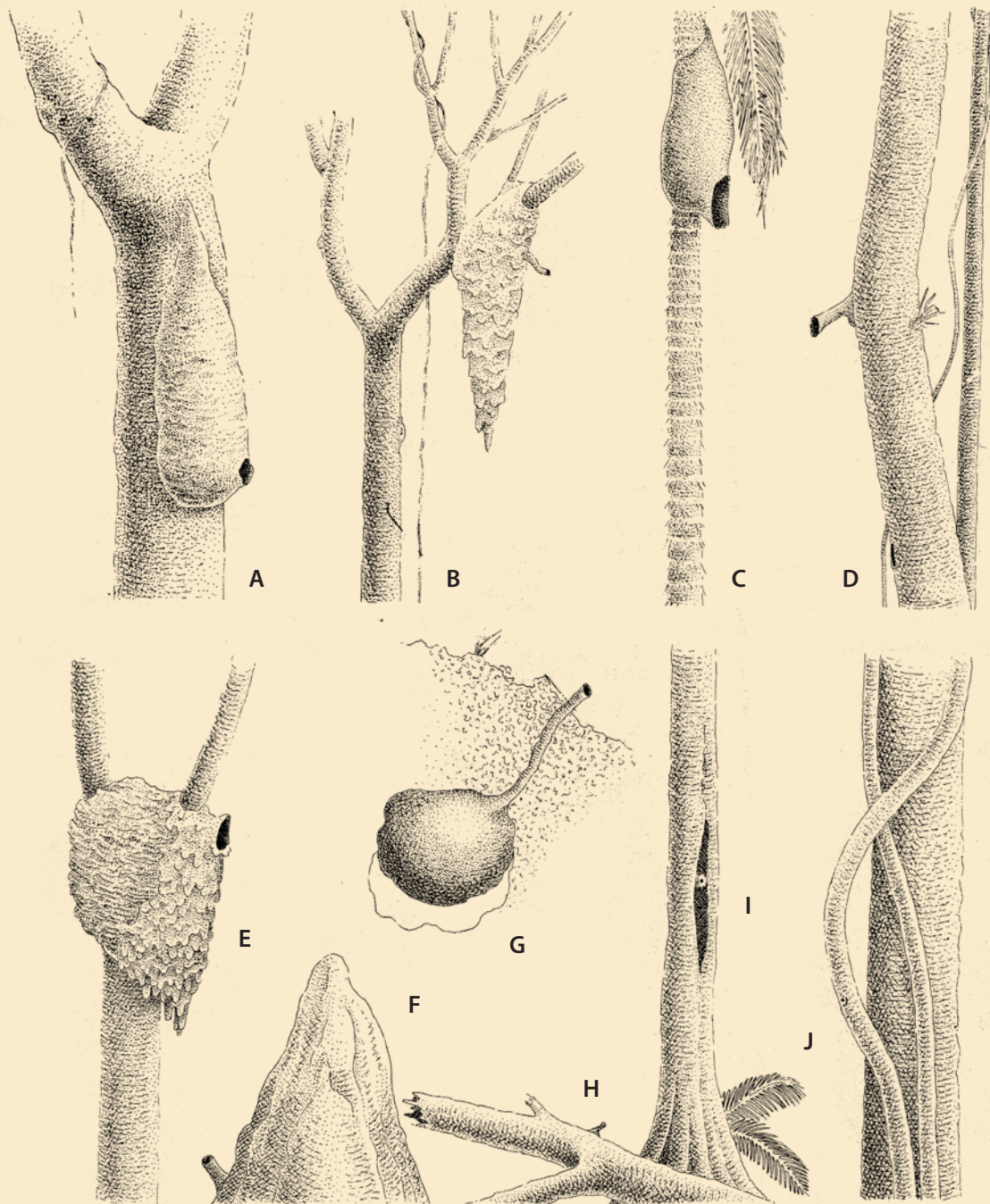


Fig. 5. Location of stingless bees recognized by the Kayapó people. **A.** *ku-krâi-ti* (*Trigona amazonensis*) has exposed nests fixed in large tree trunks or rocks in mountainous regions; **B.** *me-nô-rà-kamrek* (*Trigona cilipes*) usually builds nests in ant nests of *Azteca* sp. or in arboreal termite nests of *Nasutitermes*; **C.** *mehñy-tyk* (*Trigona branneri*) often has exposed nests fixed in the upper part of palm trunks; **D.** *imerê-ñy-kamrek* (*Scaptotrigona nigrohirta*) nests in tree hollows and the entrance tube is made with cerumen; **E.** *myre-ti* (*Partamona* cf. *cupira*) nests in arboreal termite nests; **F.** *djô* (*Trigona fulviventris*) is commonly found close to tree trunks; **G.** *puka-kan-mehn* (*Trigona recurva*), subterranean nests near termite nests; **H.** *my-krwât* (*Tetragonisca angustula*), usually nests in dead trunks near the soil; **I.** *ngài-kumrenx* (*Melipona flavolineata*), with the nest entrance hidden inside the tree hollow; **J.** *mehnô-djành* (*Frieseomelitta* sp.) nests in liana and bamboo hollow. (original drawing by J. M. F. Camargo; courtesy: Annals of Carnegie Museum (1985), Boletim do Museu Paraense Emílio Goeldi, série Zoologia 6: 17-42 (1990))

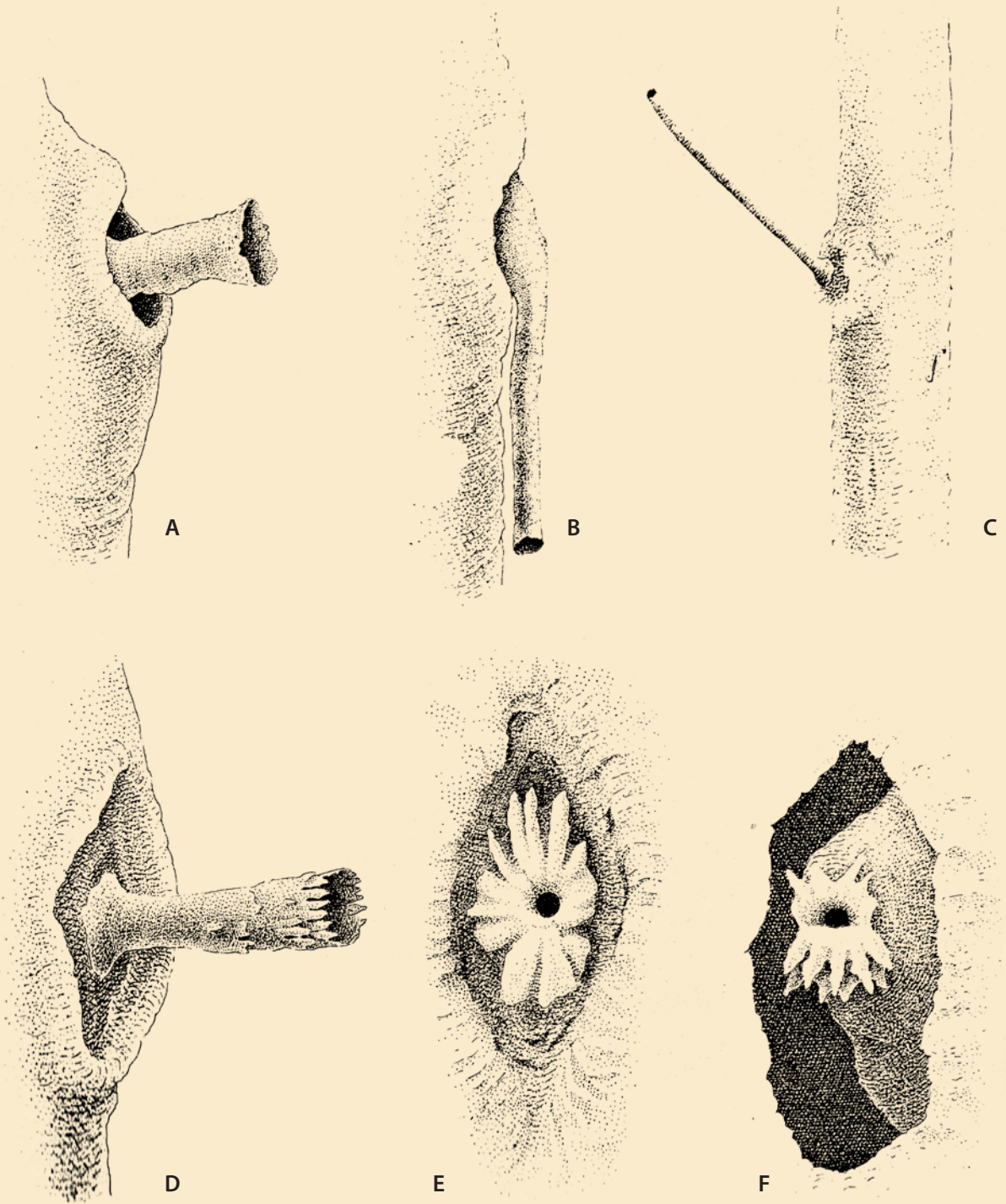


Fig. 6. Nest entrances of stingless bees recognized by the Kayapó people. **A.** *imerê-ñy-kamrek* (*Scaptotrigona nigrohirta*); **B.** *imerê-ti* (*Scaptotrigona polysticta*); **C.** *õ-i* (*Tetragona truncata*); **D.** *udjy* (*Melipona seminigra pernigra*); **E.** *menhirê-udjà* (*Melipona melanoventer*); **F.** *ngài-kumrenx* (*Melipona flavolineata*). (original drawings by J. M. F. Camargo; courtesy: Annals of Carnegie Museum (1985), Boletim do Museu Paraense Emílio Goeldi, série Zoologia 6: 17-42 (1990))

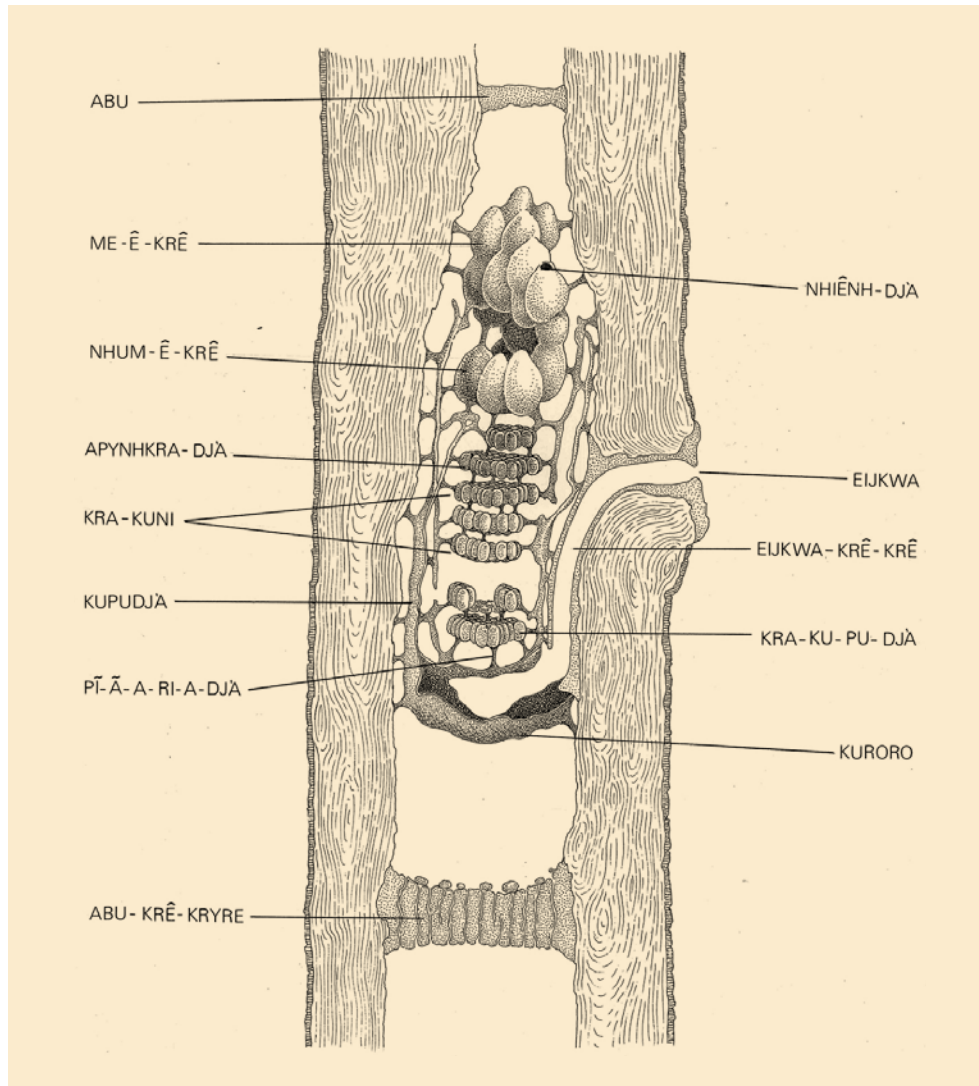


Fig. 7. Schematic representation of a *Melipona* nest and the names used by the Kayapó people: *abu* (batumen [dividing wall of a hive made of mud or wax]), *me-ê-krê* (honey pot), *apynhkra-djà* (brood cell), *kra-kuni* (brood comb), *kupudjà* (involucrum, sheets), *pi-ā-a-ri-a-djà* (supporting pillar of the combs), *abu-krê-kryre* (lower batumen for drainage), *nhiênh-djà* (open food pot), *eijkwa* (nest entrance structure), *eijkwa-krê-krê* (entrance gallery), *kra-ku-pu-djà* (cocoon) and *kuroro* (sheets, nest cover). (original drawing by J. M. F. Camargo; courtesy: Annals of Carnegie Museum (1985), Boletim do Museu Paraense Emilio Goeldi, série Zoologia 6: 17-42 (1990))

species. The edges of the recently constructed brood cells are taller than the brood cells already closed because the workers use this "collar" to seal the cells after the queen lays eggs. During this process, the liquid larval food is regurgitated into the brood cells by groups of nurse bees, after which the queen can then lay her eggs. Thus, the larva has at its disposal all the food necessary for its development and growth. This "mass

provisioning” of the brood cells – one of the main characteristics of stingless bees – comprises a liquid mixture of honey, pollen and glandular secretions of the workers and fills approximately three-quarters of the internal volume of the cell. Thus, the entire development cycle, from egg to adult stage, occurs within the brood cell, which was well known by Kayapó experts, who named each stage of development from egg to adult (Fig. 8).

The Kayapó believe that adult bees have several functions: warrior bees (*mehn-akrê*) that defend the nest; scout bees (*mehn-ô-kabin-djwynh*) who work in the field in search of food and places to establish new nests and guard the nest; and the master bee (*benadjwyrà-ratx*), who is the queen and lives in the central part of the comb, coordinating and ordering all the activities of the nest. They also recognize virgin queens (*benadjwyrà*) and brood feeders (*benadjwyrà-prõn*) as special categories.

Identification of bees

The various body parts (Fig. 9), as well as the colour of the bees and/or their wings, are important in the identification of species. The grouping of species of bees into categories allowed the identification of *imerê* (*Scaptotrigona* and *Lestrimelitta*) bees by scent, honey and cerumen and *kangàrà* (*Oxytrigona*) for their different types of defence because they burn intruders with glandular secretions. They also separate the *Trigona* spp. that build exposed arboreal nests (e.g., *T. dallatorreana* and *T. amazonensis*). The Kayapó people recognize the vegetation where bees are found (*várzea*, *igapó*, wet forest, dry forest, *cerrado*) and the preferred substrate for nesting (e.g., tree hollows, tree limbs, ant nests, and arboreal or subterranean termite nests). In these cases, the shape of the nest entrance and its smell are important for the identification of the species. They identify the flight pattern of bees around the entrance of the nest and how they defend it. They also know the species that visit dead animals, faeces and clay. In the field, they are able to identify species that nest alone on a tree, those that form clusters of nests and the possible associations between species. Of the various observations made by Camargo and Posey (1990), the following stand out:

- *Melipona flavolineata* has a very characteristic strong smell when swarming, allowing an experienced hunter to find a new nest; they produce good honey throughout the year;
- *Melipona melanoventer* is not aggressive, with very distinct noise during the night, which allows location of nests; considered semi-domesticated;
- *Melipona seminigra pernigra* is found in the high forest; is semi-domesticated and produces honey throughout the year; and is used in witchcraft.
- *Partamona cupira* is very aggressive, chases after intruders; produces little honey; and is important in medicine;

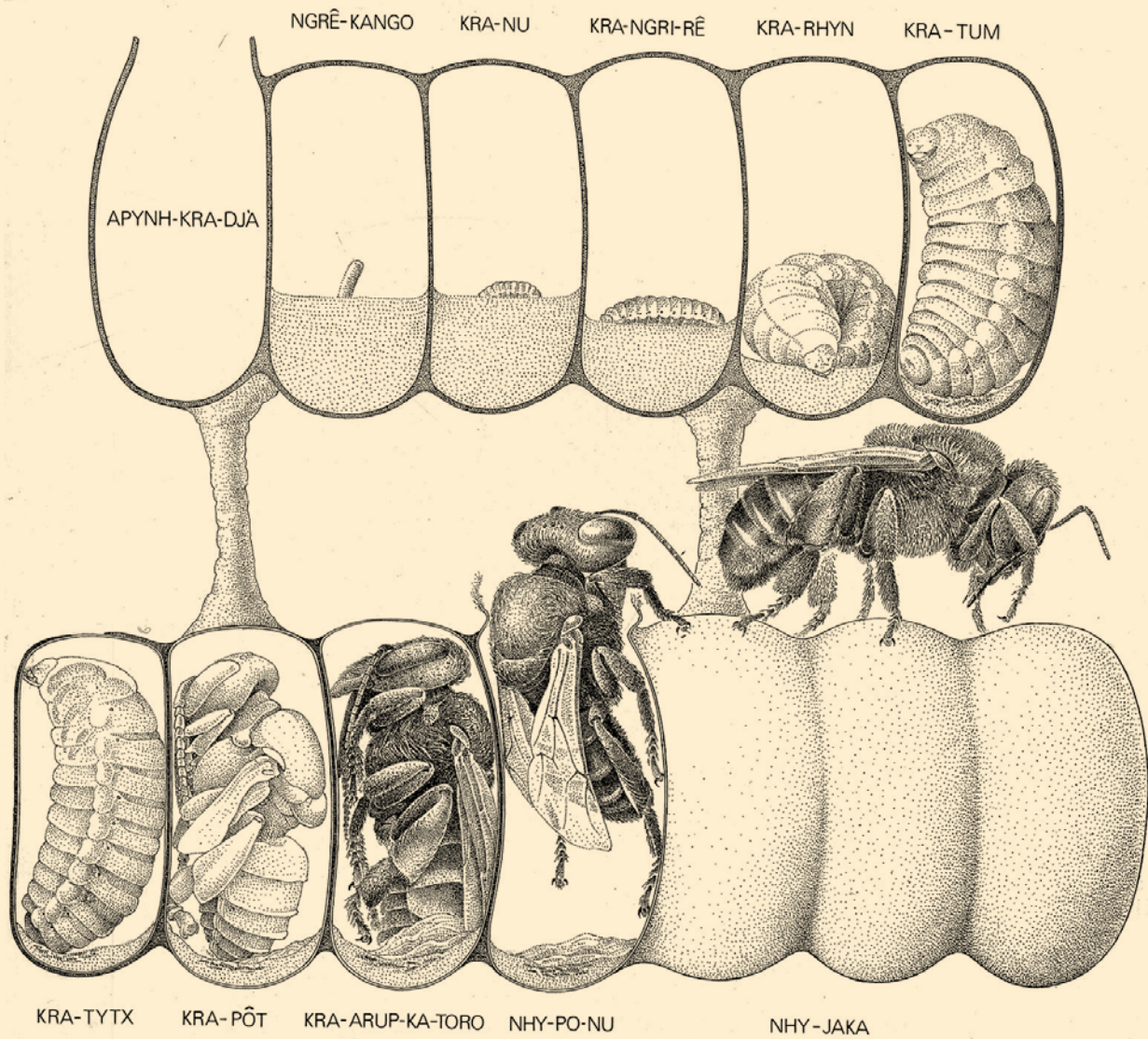


Fig. 8. Diagram of the stages of brood development, from egg to adult, for *Melipona fasciculata* (*ngai-re*). *Apynh-kra-djà* (brood cell); *ngrê-kango* (egg); *kra-nu* (first-stage larva); *kra-ngri-rê* (second-stage larva); *kra-rhyn* (pre-defecating larva, yellow larva); *kra-tum* (post-defecating larva); *kra-tytx* (prepupa); *kra-pôt* (unpigmented pupa); *kra-arup-ka-toro* (pigmented pupa, with movement); *nhy-po-nu* (emerging bee, imago); *nhy-jaka* (recently emerged bee, cleaning stage). (original drawing by J. M. F. Camargo; courtesy: Annals of Carnegie Museum (1985), Boletim do Museu Paraense Emílio Goeldi, série Zoologia 6: 17-42 (1990))

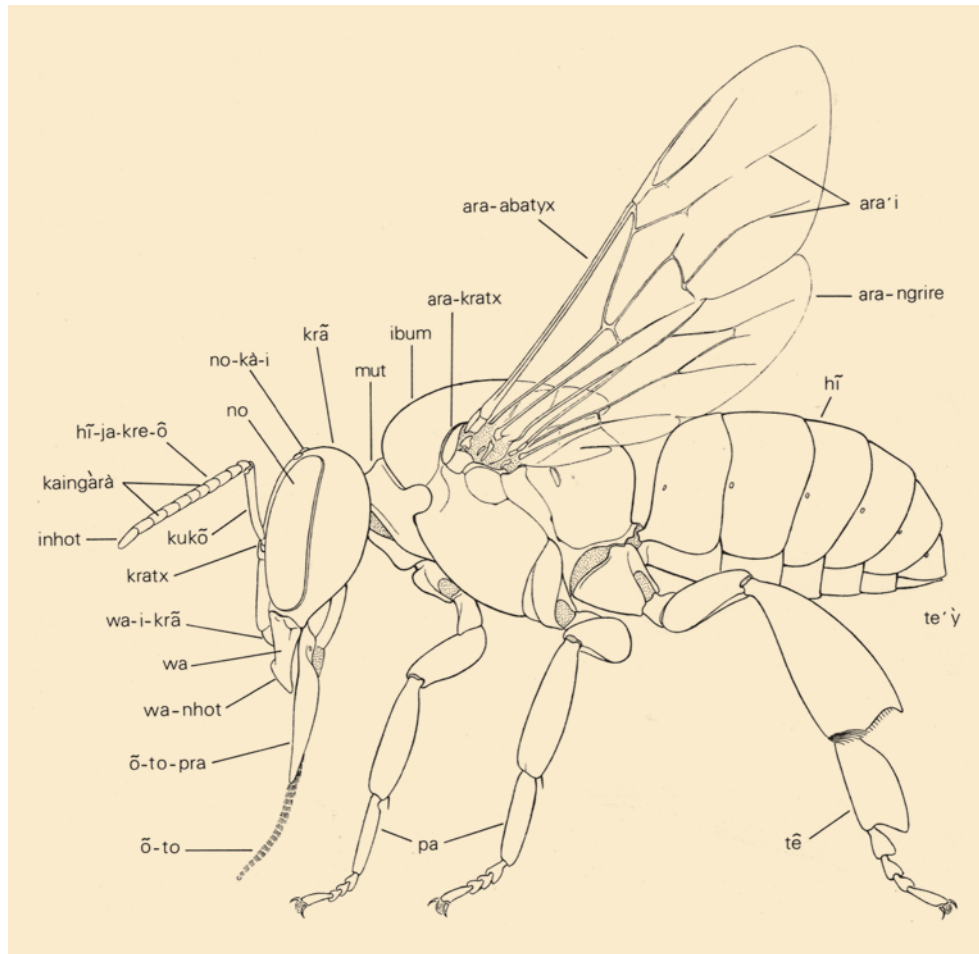


Fig. 9. Schematic representation of some morphological structures of a bee recognized by the Kayapó people: *ara-abatyx* (forewing, large wing); *ara ngrire* (small wing, hindwing); *ara-i* (wing veins), *ara-kratx* (wing joint); *krã* (head); *no-kã-i* (ocelli, simple eyes); *no* (composite eye); *hĩ-ja-kre-ô* (antenna); *kaingãrà* (antennal segments); *inhot* (end, tip); *kukô* (base of the antenna); *kratx* (joint); *wa-i-krã* (labrum); *wa* (mandible); *wa-nhot* (teeth of the mandible); *ô-to-pra* (proboscis, hanging tongue); *ô-to* (tongue), *mut* (neck, prothorax); *ibum* (back, mesothorax); *pa* (arm, front legs); *tê* (foot, hind legs); *hĩ* (abdomen); *tê-y* (tip of the abdomen). (original drawing by J. M. F. Camargo; courtesy: *Annals of Carnegie Museum* (1985), *Boletim do Museu Paraense Emílio Goeldi, série Zoologia* 6: 17-42 (1990))

- *Scaptotrigona nigrohirta* is very aggressive, bites and chases; attacks other bees by biting their wings; produces good honey throughout the year; the nest may have more than one queen; because of its sweetness, they eat pollen, if it is yellow; the cerumen is used for making the *mê-kutôm*, and only the descendants of the chiefs are named the bee (*imerê*) and own the helmets;
- *Scaptotrigona polysticta* is very docile; cerumen is also used for making the *mêkutôm*; and it produces honey in large quantities during the dry season;

- *Tetragona clavipes* throws away old honey in the dry season;
- *Tetragona dorsalis* produces a special noise when dividing its colonies in the swarming process and produces good honey throughout the year; the resins collected by the bees are used for burning, and the smoke purifies the house and the body, mainly of sick or weak people; the burned cerumen and batumen cure dizziness; and the nest can be located by the song of the towapê-tê bird (*Hypocnemis cf. cantator*), a predator of adult bees; and
- *Trigona amazonensis* is very aggressive, bites and chases and produces highly appreciated honey in large quantities during the dry season; the crushed bees are rubbed on the bodies of hunting dogs so that they remain fearless and aggressive.

The indigenous knowledge about bees does not address the pollination process itself, but the Kayapó people plant species that the bees visit because the harvests are abundant in the presence of bees. In their farmed fields, they leave logs that can be used by bees as nesting sites. They know the animals that steal honey from bees (*tayra*, *Eira barbara*, and wasps, *Polybia emaciata* and *P. sericea*). They also know the bumblebees (*kungnt*), *Bombus*, which steal only pollen.

References

- Camargo JMF, Posey DA (1990) O conhecimento dos Kayapó sobre as abelhas sociais sem ferrão (Meliponinae, Apidae, Hymenoptera): Notas adicionais. Boletim do Museu Paraense Emílio Goeldi, série Zoologia 6: 17-42.
- Campos MD'O (2006). A cosmologia dos Caiapó. In: Etnoastronomia, Scientific American Brasil, São Paulo, 14: 62-71.
- Hill R, Nates-Parra G, Quezada-Euán JJG, et al. (2019) Biocultural approaches to pollinator conservation. Nature Sustainability 2: 214-222.
- Kerr WE, Posey DA (1984) Informações adicionais sobre a agricultura dos Kayapos. Interciencia 9: 392-400.
- Posey DA (1981) Apicultura popular dos Kayapó. Revista de Atualidade Indígena 15: 105-120.
- Posey DA (1983) Keeping of stingless bees by the Kayapó indians of Brazil. Journal of Ethnobiology 3: 63-73.
- Posey DA (1985) Indigenous management of tropical forest ecosystems: the case of the Kayapó indians of the Brazilian Amazon. Agroforestry Systems 3: 139-158.
- Posey DA, Camargo JMF (1985) Additional notes in the classification and knowledge of stingless bees (Meliponinae, Apidae, Hymenoptera) by the Kayapo Indians of Gorotire (Pará, Brazil). Annals of the Carnegie Museum 54: 247-274.
- Quezada-Euán JJG, Nates-Parra G, Maués MM, et al. (2018) The economic and cultural values of stingless bees (Hymenoptera: Meliponini) among ethnic groups of tropical America. Sociobiology 65: 534-557.

Lifestyle diversity of Amazonian bees

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The stingless bees (Apidae, Meliponini) comprise a highly diverse group concerning body size, colony size, nesting biology, and behaviour (Michener, 1974; Roubik, 1989; Pedro, 2014). Approximately 75% of the species described for the Brazilian territory (177 out of 244 species) have been registered in the Amazon Rainforest (Pedro, 2014), which highlights the leading role of this biome for the country's biodiversity. The elevated richness of meliponine species, and the consequent competition over resources and nesting space, gave rise to a rich variety of different lifestyles among the Amazonian stingless bees. Yet, the biology of most species has remained largely unknown to this date, which is mainly due to the difficulty in access their natural habitats.

On his expeditions to the Amazon Rainforest, João Camargo collected detailed information on the occurrence of stingless bees in this biome and described meticulously the morphological features of the individuals and the characteristics of each species' nest architecture. Moreover, being a holistic naturalist, he made important observations on several biological peculiarities of the meliponines of the Amazon region. Many of these had been unprecedented and unexpected for social bees, such as the mutualistic association with wax-producing scale insects (Camargo and Pedro, 2002a, b), the storage of pollen together with yeast (Camargo and Pedro, 2004), the complete absence of food storage (Camargo and Pedro, 2007), the storage of resins in specialized pots (Camargo and Pedro, 2004), the specialisation in robbing resources from the nests of other bee species (Camargo and Moure, 1989; Camargo and Pedro, 2008), and necrophagy (Camargo and Roubik, 1991). These observations formed the solid basis for a variety of studies by national and international research teams, thus underlining their scientific importance and relevance.

The mutualistic association with scale insects in *Schwarzula* spp.

Scale insects (Hemiptera, Coccoidea) are small hemipterans, usually measuring less than 5 mm, that feed on the saps of their host plants (Gullan and Kosztarab, 1997). In most species, the insects secrete wax, covering the entire body with a protective layer (Tamaki et al., 1969). This wax shield, which amounts to approximately 75% of the individuals' body mass, resembles the scales of fish or reptiles, which coined the common name of these bugs (Gullan and Kosztarab, 1997). In addition to wax, the animals excrete a solution composed of carbohydrates and amino acids (Way, 1963) that attracts ants and bees (Way, 1963; Santos et al., 2019).

Stingless bees, usually, collect both the sugary solution and the wax secreted by the scale insects opportunistically, when encountering agglomerations of these hemipterans on their respective host plants (Cortopassi-Laurino, 1977; Santos et al., 2019). An exceptional case in this context are the meliponine species *Schwarzula timida* and *S. coccidophila* (Camargo and Pedro, 2002b). In strict contrast to the opportunistic associations with scale insects, known for various stingless bees, colonies of *Schwarzula* herd groups of more than 200 coccids in the galleries of their nests (Camargo and Pedro, 2002a), where they harvest both the sugary solution and the wax produced by the hemipterans. The basitarsi and the mandibles of the workers of *Schwarzula*, used in wax collection and transport, are modified in comparison to phylogenetically closely related species (Camargo and Pedro, 2002a, b). After the harvest, the bees stock the wax in specific deposits for posterior use as material in nest construction. The sugary secretions of the coccids are stored in the honey pots and, presumably, are the main source of carbohydrates for the colonies of *Schwarzula*, given that the foragers collect mainly pollen and secretions rich in salt (Camargo and Pedro, 2002a). In exchange for providing resources for the bees, the scale insects receive shelter and protection against predators.

Mutualistic associations between scale insects and social insects are well known in ants, which guard agglomerations of these hemipterans on their host plants in exchange for the sugary secretions (Way, 1963). However, only few ant species rear and maintain coccids within their nests (Flanders, 1957) as observed in *Schwarzula*, which highlights the exceptionality of this biological characteristic for social insects.

The peculiar stocks of *Ptilotrigona lurida*

Social bees with perennial colonies, such as the stingless bees, collect food when it is abundant in the environment and stock it in the nest to overcome dearth periods (Michener, 1974; Hrncir et al., 2019). The food products harvested comprise carbohydrates (mainly nectar) as energy supply for the adults, and proteins (usually pollen) as key nutrient for the larvae (Michener, 1974). As has been demonstrated in honey bees (*Apis mellifera*), a colony's tendency to collect more or less pollen is

determined genetically (Hunt et al., 1995). Given that pollen is the main source of proteins for larval development, brood production and, consequently, population size of a colony increases with increasing foraging effort for this resource (Page and Fondrk, 1995).

In addition to variations in brood production over the year, associated with pollen availability in the field (Roubik, 1982a; Maia-Silva et al., 2015), stingless bee species differ concerning their pollen foraging activity (Leonhardt et al., 2007), which may explain differences in colony size between species, varying from a few dozens to tens of thousands workers (Wille, 1983). An interesting case in this context is *Ptilotrigona lurida*, one of the most conspicuous and aggressive stingless bee species of the Amazon region (Camargo et al., 1992; Camargo and Pedro, 2004). In general, the nests of this species are huge, and worker populations may comprise more than 20,000 individuals (Camargo et al., 1992; Camargo and Pedro, 2004). One of the peculiarities of *P. lurida* is the exuberant pollen storage in the nests, which may reach up to more than 2 kg. The stored pollen is extremely dry, and it is even possible to distinguish the individual pollen loads deposited by the foragers (Camargo et al., 1992). Usually, the pollen storage contains *Candida* yeast that causes dehydration of the stored food, therewith increasing its durability (Camargo et al., 1992). Moreover, the fungi hamper or even impede the infestation of the pollen pots by phorid flies, well-known parasites in stingless bee colonies that feed on the colonies' pollen storage (Camargo et al., 1992). Recent studies point to additional advantages of such mutualistic associations between meliponine bees and fungi: *Zygosaccharomyces* sp. yeast produce steroids that have a key function in the metamorphosis of the larvae in *Scaptotrigona depilis* (Paludo et al., 2018). Thus, the colonies need to cultivate these fungi to facilitate the complete development of the individuals and, consequently, promote colony survival (Menezes et al., 2015). Interactions between different types of yeast, common in the food storage pots of stingless bees, may stimulate (*Candida* sp.) or inhibit (*Monascus ruber*) the growth of *Zygosaccharomyces* sp., therewith modulating the larval development of the colonies (Paludo et al., 2019).

Another peculiarity of *P. lurida* is that honey pots are rare or even absent. On the other hand, the nests contain a considerable number of pots that contain resins, particularly from flowers of *Clusia* spp. (Camargo et al., 1992; Camargo and Pedro, 2004) that offer resins as reward for pollinators (Mesquita and Franciscon, 1995). Stingless bees collect this resource as raw material for nest construction or for nest defence (Roubik, 2006; Leonhardt et al., 2010) and, usually, store it in small resin deposits on the nest's wall or between the layers of the involucre (Roubik, 2006). Thus, the way *P. lurida* stores this resource is unique among the meliponines. The large stocks of *Clusia* spp. resins may be associated with the conservation of yeast in the pollen pots. Plant resins, typically, show a strong antimicrobial activity (Drescher et al., 2014). However, *Clusia* spp. resins, although inhibiting the growth of bacteria, have no effect on yeasts (Lokvam and Braddok, 1999). Thus, by using this type of resin in the construction of food storage pots and brood cells (Camargo and Pedro, 2004), colonies of *P. lurida* may facilitate the growth of yeast in pollen pots that are free of any bacterial contamination.



A. *Ptilotrigona lurida* nest entrance. **B.** Pollen pellets dehydrated by *Candida* sp. (photos: J. M. F. Camargo; Coleção Entomológica "Prof. J. M. F. Camargo")

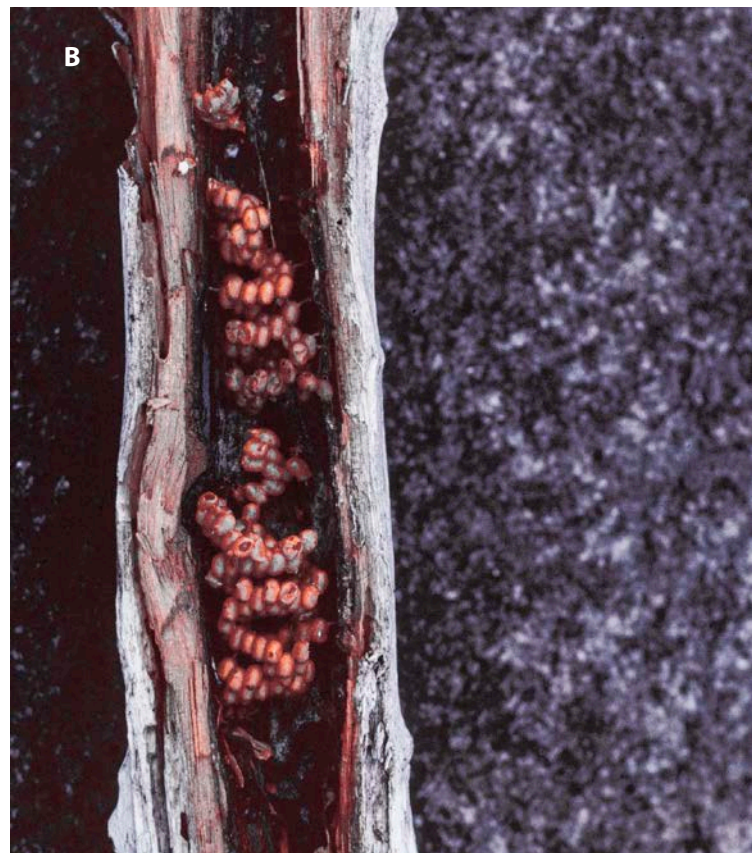
The absence of food storage in *Trichotrigona* spp.

Contrasting the premise that food storage is crucial for maintaining perennial colonies, food storage pots are completely missing in nest of *Trichotrigona extranea* (Camargo and Moure, 1983; Camargo and Pedro, 2007) and *T. camargoiana* (Pedro and Cordeiro, 2015). Both these meliponine species have small colonies, comprising between several dozens to few hundreds of adult workers. On most occasions, their nests were found close to those of *Frieseomelitta* spp., or even sharing the same tree cavity, separated by hard and compact layers of batumen (Camargo and Moure, 1983; Camargo and Pedro, 2007; Pedro and Cordeiro, 2015). Even though *Trichotrigona* bees, just as other meliponines, provision their brood cells with pollen (Camargo and Pedro, 2007), foragers returning with pollen loads on their corbiculae have not been observed so far (Pedro and Cordeiro, 2015). Presumably, the workers carry pollen together with nectar inside their honey stomach and use this mixture directly for brood cell provisioning (Pedro and Cordeiro, 2015). The absence of any type of food storage pots together with the reduction of body structures associated with the collection and manipulation of pollen (Camargo and Pedro, 2007; Pedro and Cordeiro, 2015) suggests a cleptobiotic lifestyle of *Trichotrigona* spp.

Cleptobiosis, the robbing of resources from the nests of other bee species, is a behaviour well known for the meliponine genus *Lestrimelitta* (Nogueira-Neto, 1970; Wittmann et al., 1990; Sakagami et al., 1993). Yet, in contrast to *Trichotrigona* spp., the colonies of *Lestrimelitta* spp. contains several thousand individuals, and the invasion of the nests of other stingless bee species occurs in mass attacks (Nogueira-Neto, 1970; Sakagami et al., 1993) coordinated through pheromones (Wittmann et al., 1990). The robbers quickly plunder the entire pollen and honey stock as well as the brood's food provisions of the host colonies, and carry their loot within the honey stomach to their own nests, where they store the resources in pots of mixed content (Sakagami and Laroca, 1963; Quezada-Euán and González-Acereto, 2002).

A. *Trichotrigona extranea* nest entrance. **B.** Internal view of the nest, showing the brood combs and the lack of food pots. (photos: J. M. F. Camargo; Coleção Entomológica "Prof. J. M. F. Camargo")

All species of the genus *Lestrimelitta* have an obligate cleptobiotic lifestyle, which means that they do not collect any food at flowers and, consequently, the survival of the colonies depends solely on the success of their raids (Nogueira-Neto, 1970). However, some meliponine species



loot the nests of other social bees facultatively, among them *Melipona fuliginosa*, one of the biggest stingless bees (Cortopassi-Laurino, 2004; Camargo and Pedro, 2008). The colonies of this species are populous, containing approximately one thousand adult individuals, and show aggressive nest defence (Cortopassi-Laurino, 2004). *M. fuliginosa* colonies plunder the nests of other social bees in the close neighbourhood. The raids, during which the invaders steal mainly honey and wax, may go on for several days and, frequently, cause severe damage or even lead to the death of the colonies attacked (Costa et al., 2018). However, workers of *M. fuliginosa* also forage for nectar and pollen at flowers (Cortopassi-Laurino, 2004). Only when floral abundance is low, the colonies switch to opportunistic nest raiding (Costa et al., 2018).

Just like the species of *Lestrimelitta*, colonies of *M. fuliginosa* deposit the food, collected at flowers or robbed from other nests, in storage pots (Camargo and Pedro, 2008), which highlights the singularity of the absence of food storage in *Trichotrigona* (Camargo and Moure, 1983; Camargo and Pedro, 2007; Pedro and Cordeiro, 2015). A possible explanation for this peculiar feature is the reduced need for hoarding food owing to the small number of adults and the low brood cell production by the colonies. However, both the true cause for the absence of food storage pots in *Trichotrigona* spp. and their cleptobiotic lifestyle have remained open questions to this day.

Necrophagy

Curiously, many stingless bee genera (*Camargoia*, *Cephalotrigona*, *Frieseomelitta*, *Geotrigona*, *Melipona*, *Nannotrigona*, *Oxytrigona*, *Paratrigona*, *Partamona*, *Plebeia*, *Scaptotrigona*, *Scaura*, *Tetragona*, *Trigona* and *Trigonisca*) visit the carcasses of dead animals, where they collect liquids and small pieces of meat (Müller, 1874; Cockerell, 1920; Schwarz, 1948; Cornaby, 1974; Baumgartner and Roubik, 1989; Lorenzon and Matrangolo, 2005). The collection of animal proteins by social insects is well known from wasps and ants (Reed, 1958). Initially, this behaviour, peculiar for bees, was thought to be associated with the collection of nest construction material (Schwarz, 1948; Wille, 1983). Yet, foraging at animal carcasses may have alternative explanations. First, the bees obtain important salts and minerals from the collected liquids (Baumgartner and Roubik, 1989). Second, similarly to wasps and ants, they may use the meat itself as protein supplement for feeding the larvae (Roubik, 1989; Noll et al., 1996).

In this context, a unique meliponine group are the obligate necrophagous bees, *Trigona hypogea*, *T. necrophaga* e *T. crassipes*. In strict contrast to facultative necrophages, these stingless bee species do not visit flowers for food (Camargo and Roubik, 1992; Noll et al., 1996). The colonies obtain their carbohydrates, stored in honey pots, from liquids with high sugar content, collected at fruits of extrafloral nectaries (Camargo and Roubik, 1992; Noll et al., 1996). An interesting morphological feature of the obligate necrophages is the complete absence of corbiculae in workers (Roubik, 1982b; Camargo and Roubik, 1991), which indicates that these bees lost any capacity to collect pollen at

flowers. Thus, meat, collected at animal carcasses, is the exclusive source of proteins for these stingless bees (Roubik, 1982b). When the scouts find a recently dead animal, they quickly recruit many additional foragers (Jarau et al., 2003) that remove fur, or plumage, and skin from the carcass (Roubik, 1982b). Thereafter, they cut pieces of meat with their strong mandibles, and chew them for several minutes prior to carrying the resulting, pasty material in their honey stomach to the nest (Gilliam et al., 1985; Camargo and Roubik, 1991). Subsequently, the foragers deposit the pre-digested meat in special pots that contain a viscous mixture of animal protein and honey (Camargo and Roubik, 1991; Noll et al., 1996).

In the tropics, the meat of dead animals rots quickly if not conserved appropriately. Thus, the long-term storage of animal proteins represents a challenge for bees. The necrophagous species solve this problem through chemical transformations of the stored protein (Noll et al., 1996). After filling a storage pot, it is sealed by the workers, and the mixture of pre-digested animal protein and honey matures for about two weeks within the closed environment. During this maturation process, the quantity of soluble proteins diminishes as the content of amino acids and sugars increases, and the pasty material is transformed into a homogenous viscous liquid (Noll et al., 1996). This chemical conversion, presumably, is mediated by *Bacillus* spp. bacteria, whose enzymatic activity accelerates the metabolic conversion of proteins and lipids, yet has little effect on carbohydrates (Gilliam et al., 1985). In addition to enzymes, *Bacillus* spp. produce antibiotic substances (Katz e Demain, 1977) that inhibit the occurrence of other microorganisms in the storage pots (Gilliam et al., 1985) and, consequently, conserve the animal protein over long time periods.

References

- Baumgartner DL, Roubik DW (1989) Ecology of necrophilous and filth-gathering stingless bees (Apidae: Meliponinae) of Peru. *Journal of Kansas Entomological Society* 62: 11-22.
- Camargo JMF, Moure JS (1983) *Trichotrigona*, um novo gênero de Meliponinae (Hymenoptera, Apidae) do Rio Negro, Amazonas, Brasil. *Acta Amazonica* 13: 421-429.
- Camargo JMF, Moure JS (1989) Duas espécies novas de *Lestrimelitta* Friese (Meliponinae, Apidae, Hymenoptera) da região amazônica. *Boletim do Museu Paraense Emílio Goeldi, série Zoologia* 5:195-212.
- Camargo JMF, Pedro SRM (2002a) Mutualistic association between a tiny Amazonian stingless bee and a wax-producing scale insect. *Biotropica* 34: 446-451.
- Camargo JMF, Pedro SRM (2002b) Uma espécie nova de *Schwarzula* da Amazônia (Hymenoptera, Apidae, Meliponini). *Iheringia* 92: 101-112.
- Camargo JMF, Pedro SRM (2004) Meliponini Neotropicais: o gênero *Ptilotrigona* Moure (Hymenoptera, Apidae, Apinae). *Revista Brasileira de Entomologia* 48: 353-377.
- Camargo JMF, Pedro SRM (2007) Notas sobre a bionomia de *Trichotrigona extranea* Camargo & Moure (Hymenoptera, Apidae, Meliponini). *Revista Brasileira de Entomologia* 51: 72-81.

- Camargo JMF, Pedro SRM (2008) Revisão das espécies de *Melipona* do grupo *fuliginosa* (Hymenoptera, Apoidea, Apidae, Meliponini). *Revista Brasileira de Entomologia* 52: 411-427.
- Camargo JMF, Roubik DW (1991) Systematics and bionomics of the apoid obligate necrophages: the *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biological Journal of the Linnean Society* 44: 13-39.
- Camargo JMF, Gracia MVB, Queiroz Junior ER, Castrillon A (1991) Notas prévias sobre a bionomia de *Ptilotrigona lurida* (Hymenoptera, Apidae, Meliponinae): associação de leveduras em pólen estocado. *Boletim do Museu Paraense Emílio Goeldi, série Zoologia* 8: 391-395.
- Cockerell TDA (1920) Some neotropical Meliponid bees. *Bulletin of the American Museum of Natural History* 42: 459-468.
- Cornaby BW (1974) Carrion reduction by animals in contrasting tropical habitats. *Biotropica* 6: 51-63.
- Cortopassi-Laurino M (1977) Notas sobre associações de *Trigona (Oxytrigona) tataira* (Apidae, Meliponinae). *Boletim de Zoologia da Universidade de São Paulo* 2: 183-187.
- Cortopassi-Laurino M (2004) A urucu boi da Amazônia, *Melipona fuliginosa* Lepeletier, 1836. *Mensagem Doce* 77:1-3.
- Costa L, Galaschi-Teixeira JS, Maia UM, Imperatriz-Fonseca VL (2018) Plasticity of stingless bee *Melipona fuliginosa* Lepeletier to obtain food resources in Amazonia. *Sociobiology* 65:744-750.
- Drescher N, Wallace HM, Katouli M, Massaro CF, Leonhardt SD (2014) Diversity matters: how bees benefit from different resin sources. *Oecologia* 176: 943-953.
- Flanders SE (1957) The complete interdependence of an ant and a coccid. *Ecology* 38: 535-536.
- Gilliam M, Buchmann SL, Lorenz BJ, Roubik DW (1985) Microbiology of the larval provisions of the stingless bee, *Trigona hypogea*, an obligate necrophage. *Biotropica* 17: 28-31.
- Gullan PJ, Kosztarab M (1997) Adaptations in scale insects. *Annual Review of Entomology* 42: 23-50.
- Hrncir M, Maia-Silva C, Teixeira-Souza VHS, Imperatriz-Fonseca VL (2019) Stingless bees and their adaptations to extreme environments. *Journal of Comparative Physiology A* 205: 415-426.
- Hunt GJ, Page RE, Fondrk MK, Dullum CJ (1995) Major quantitative trait loci affecting honey bee foraging behavior. *Genetics* 141: 1537-1545.
- Jarau S, Hrncir M, Schmidt VM, Zucchi R, Barth FG (2003) Effectiveness of recruitment behavior in stingless bees (Apidae, Meliponini). *Insectes Sociaux* 50: 365-374.
- Katz E, Demain AL (1977) The peptide antibiotics of *Bacillus*: chemistry, biogenesis, and possible functions. *Bacteriological Reviews* 41: 449-474.
- Leonhardt SD, Dworschak K, Eltz T, Blüthgen N (2007) Foraging loads of stingless bees and utilisation of stored nectar for pollen harvesting. *Apidologie* 38: 125-135.
- Leonhardt SD, Jung L-M, Schmitt T, Blüthgen N (2010) Terpenoids tame aggressors: role of chemicals in stingless bee communal nesting. *Behavioral Ecology and Sociobiology* 64: 1415-1423.
- Lokvam J, Braddock JF (1999) Anti-bacterial function in the sexually dimorphic pollinator rewards of *Clusia grandiflora* (Clusiaceae). *Oecologia* 119: 534-540.
- Lorenzon MCA, Matrangolo CAR (2005) Foraging on some nonfloral resources by stingless bees (Hymenoptera, Meliponini) in a caatinga region. *Brazilian Journal of Biology* 65: 291-298.
- Maia-Silva C, Hrncir M, Silva CI, Imperatriz-Fonseca VL (2015) Survival strategies of stingless bees (*Melipona subnitida*) in an unpredictable environment, the Brazilian tropical dry forest. *Apidologie* 46: 631-643.

- Menezes C, Vollet-Neto A, Marsaioli AJ, et al. (2015) A Brazilian social bee must cultivate fungus to survive. *Current Biology* 25: 2851-2855.
- Mesquita RCG, Franciscon CH (1995) Flower visitors of *Clusia nemorosa* G. F. W. Meyer (Clusiaceae) in an Amazonian whitesand campina. *Biotropica* 27: 254-257.
- Michener CD (1974) The social behavior of the bees. Cambridge: Harvard University Press.
- Müller H (1874) Larvae of membracis serving as milk-cattle to a Brazilian species of honey-bees. *Nature* 8: 31-32.
- Nogueira-Neto P (1970) Behavior problems related to the pillages made by some parasitic stingless bees (Meliponinae, Apidae). In: Aronson LR (ed.) Development and evolution of behavior: Essays in memory of TC Schneirla. WH Freeman, San Francisco, pp. 416-434.
- Noll FB, Zucchi R, Jorge JA, Mateus S (1996) Food collection and maturation in the necrophagous stingless bee, *Trigona hypogea* (Hymenoptera: Meliponinae). *Journal of Kansas Entomological Society* 69: 287-293.
- Page RE, Fondrk MK (1995) The effects of colony-level selection on the social organization of honey bee (*Apis mellifera* L.) colonies: colony-level components of pollen hoarding. *Behavioral Ecology and Sociobiology* 36: 135-144.
- Paludo CR, Menezes C, Silva-Junior EA, et al. (2018) Stingless bee larvae require fungal steroid to pupate. *Scientific Reports* 8: 1122.
- Paludo CR, Pishchany G, Dominguez A, et al. (2019) Microbial community modulates growth of symbiotic fungus required for stingless bee metamorphosis. *PLoS ONE* 14:e0219696.
- Pedro SRM (2014) The stingless bee fauna in Brazil (Hymenoptera: Apidae). *Sociobiology* 61:348-354.
- Pedro SRM, Cordeiro GD (2015) A new species of the stingless bee *Trichotrigona* (Hymenoptera: Apidae, Meliponini). *Zootaxa* 3956: 389-402.
- Quezada-Euán JG, González-Acereto JA (2002) Notes on the nest habits and host range of cleptobiotic *Lestrimelitta niitkib* (Ayala 1999) (Hymenoptera: Meliponini) from the Yucatan peninsula, Mexico. *Acta Zoologica Mexicana* 86: 245-249.
- Rech AR, Schwade MA, Schwade MRM (2013). Abelhas sem ferrão amazônicas defendem meliponíneos contra saques de outras abelhas. *Acta Amazonica* 43: 389-394.
- Reed HB (1958) A study of dog carcass communities in Tennessee, with special reference to the insects. *American Midland Naturalist* 59: 213-245.
- Roubik DW (1982a) Seasonality in colony food storage, brood production and adult survivorship: studies of *Melipona* in tropical forest (Hymenoptera: Apidae). *Journal of Kansas Entomological Society* 55: 789-800.
- Roubik DW (1982b) Obligate necrophagy in a social bee. *Science* 217: 1059-1060.
- Roubik DW (1989) Ecology and natural history of tropical bees. New York: Cambridge University Press.
- Roubik DW (2006) Stingless bee nesting biology. *Apidologie* 37: 124-143.
- Santos CF, Halinski R, Santos PDS, et al. (2019) Looking beyond the flowers: associations of stingless bees with sap-sucking insects. *The Science of Nature* 106: 12.
- Sakagami SF, Laroca S (1963) Additional observations on the habits of the cleptobiotic stingless bees, the genus *Lestrimelitta* Friese (Hymenoptera, Apoidea). *Journal of Faculty of Science, Hokkaido University* 15: 319-339.

- Sakagami SF, Inoue J, Yamane S, Salmah S (1989) Nests of the myrmecophilous stingless bee *Trigona moorei*: how do bees initiate their nest within an arboreal ant nest? *Biotropica* 21: 265-274.
- Sakagami SF, Roubik DW, Zucchi R (1993) Ethology of the robber stingless bee *Lestrimelitta limao* (Hymenoptera Apidae). *Sociobiology* 21:237-277.
- Schwarz HF (1948) The stingless bees of the Western Hemisphere. *Bulletin of the American Museum of Natural History* 90: 1-546.
- Tamaki Y, Yushima T, Kawai S (1969) Wax secretion in a scale insect, *Ceroplastes pseudoceriferus* Green (Homoptera: Coccidae). *Applied Entomology and Zoology* 4: 126-134.
- Way MJ (1963) Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology* 8: 307-344.
- Wille A (1983) Biology of the stingless bees. *Annual Review of Entomology* 28: 41-64.
- Wittmann D, Radtke R, Zeil J, Lübke G, Francke W (1990) Robber bees (*Lestrimelitta limao*) and their host chemical and visual cues in nest defense by *Trigona (Tetragonisca) angustula* (Apidae: Meliponinae). *Journal of Chemical Ecology* 16: 631-641

The nests of stingless bees, from nature to museums

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*Instituto Tecnológico Vale – Desenvolvimento Sustentável
and Universidade de São Paulo*

In nature, the nests of stingless bees (Meliponini) can be found in different substrates. They occupy pre-existing cavities in living or dead trees, in the ground, and the nest of other social insects, including ants, termites, and sometimes even wasps. Lianas may also serve as a nesting substrate. Some stingless bee species, like those from the genus *Trigona*, built exposed nests.

The expeditions of João M. F. Camargo to the Amazon region allowed the detailed study of stingless bees with vastly different nesting habits and nest architecture. Despite the diversity in many behavioural aspects, all stingless bee species share the same general nesting pattern, characterised through brood cells, constructed by the workers with mixtures of wax and resin (called cerumen) and provisioned with all food necessary for the larval development, followed by the queen's oviposition. The brood cells are used only once and are destroyed as soon as the new bees emerge from them. Honey and pollen are stored in food pots.

The nests presented in the following compilation, clearly evidence the rich information on stingless bee species previously unknown to science. The detailed study of the bees' nest architecture shows diversity in size and shape and points to behaviours unknown before. After the expeditions, series of nest specimens and, others, conserved in liquid had been deposited at the entomological collection "Coleção Entomológica da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo (FFCLRP-USP)", today named Coleção Entomológica "Prof. J. M. F. Camargo". The collection as well comprises the nest entrances, meticulously described and drawn in every detail. They are fundamental for the identification of the particular stingless bee species. Hence, when available, images of the nest entrances are provided in the following compilation.

The plates of the stingless bees portrayed in this book show a worker of each species collected in the State of Pará so that they can be identified through specialised identification keys or for comparison. Each bee, or specimen, receives several labels on its origin and identification. One of these indicates the location at which the bee had been collected and by whom. Another tag provides information on who identified the species. All this information is crucial to certificate the identity of the individual bee species, and, therefore, the labels are presented in the plates together with the bees.

We call it a catalogue when all information on a given species is compiled in a database. This information includes, among others, the list of world museums and collections with specimens under the given specific name and the number of existent samples in each museum where this species has been listed. Currently, these databases are linked to images and other existing data. Once available in digital form, this information will facilitate the species identification, given that the original material of the collections is precious and access is granted, mostly, only to specialist researchers. For stingless bees, João M. F. Camargo and Sílvia R. M. Pedro revised the content of all collections as well as the bibliography available until 2004 for their contribution on stingless bees in the Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region (Camargo and Pedro, 2013).

All data of the Coleção Entomológica “Prof. J. M. F. Camargo” were made available for public access through the project “*Distributed information system for biological collections, the integration of Species Analyst and SinBiota*”, with financial support from the São Paulo Research Foundation (FAPESP) in its initial stage in 2005.

The Coleção Entomológica “Prof. J. M. F. Camargo” has been reorganised by the current curator Prof. Eduardo A. B. de Almeida. The digitisation of the information was made possible with the help of Dr. Fábio B. Quinteiro and Dr. Anne M. Costa, both financially supported by the Instituto Tecnológico Vale – Desenvolvimento Sustentável (ITV-DS). The complete digitised photo library has also been made publicly available by the *Scientific information system about neotropical bees*. The specimens studied in research performed by the ITV-DS have been deposited in the collection of the Museu Paraense Emílio Goeldi.

Studies on the bees of Carajás performed by the ITV-DS

We have two main lines of research on bees from Serra dos Carajás in the State of Pará. The first is an inventory of pre-existing information on the local bee diversity (including all bee species, not only the stingless bees) and bee collections in the field. The second line includes studies on the local stingless bee species and their nests that could be rescued during ongoing processes of removal of native vegetation (Costa, 2019).

Research projects by the ITV-DS have studied various aspects of the bees in the National Forest of Carajás. The first step was to establish a list of species previously described for the region, using online data providers like speciesLink (open access)

as well as the ITV-DS institutional database. This preliminary list was compared with specimens deposited in two entomological collections, the collection of Museu Paraense Emílio Goeldi and the collection of the Universidade Federal de Minas Gerais that has a section for insects from Carajás. These data, together with the previously collected species, were crucial for establishing a list of species, for which we now have a robust and reliable database. For these species we determined several functional characteristics – such as body size, nesting habit, sociality, whether they are known as crop pollinators or not – that allow more detailed analyses of the main functions and ecosystem services provided by the different species in nature.

The next step was new collections of bees in the field. For these, we used standard methods for insect collections in areas of *canga* vegetation in Carajás, which are vegetational islands isolated from the Amazon Rainforest vegetation. In each region, we collected bees in standardised surveys using different methodological approaches (insect nets, olfactory traps, trap nests). Moreover, to understand the relationship between bees and plants in these natural environments, we determined patterns of interaction between bees and flowers. These interactions constitute complex networks that allow very insightful analyses concerning the conservation ecology of the involved species. In addition to the surveys in the areas with *canga* vegetation, we collect bees in after mining recovery zones for comparisons of bee diversity and bee-plant interactions with control areas with original forest vegetation. Thus, we continuously add new information to the initial knowledge, including new bee species and their interactions with plants, an essential piece of information that has been missing so far. All this information is crucial for establishing strategies to restore degraded areas, which includes not only the recovery of species but the restoration of the interactions between the plants and their pollinators.

Based on the structured data, it was possible to evaluate the potential impact of climate changes on the bees that occur at Carajás. These species represent approximately 80% of all species reported for the State of Pará and, therefore, are a useful reference for the potential impact of the ongoing climate change on the bee communities in the region. The results suggest that more than 85% of the species at Carajás may not find appropriate habitats in the future. This effect is more significant for species known to pollinate crops as well as for species with very restricted geographic distribution. However, some regions show a more stable climate situation, particularly areas to the west and north of Carajás. These regions may be considered climatic refuges that will be key to protect native species in the future.

Moreover, we tried to determine the ecosystem service value of pollination by bees in the State of Pará. For this, we analysed crops in various municipalities of the state, many of which depend to a high degree on bees for their productivity. Some of the plants are particularly important for the economy of the municipalities, such as açai, which yields hugely high profits and depends on bee pollination. Studies like these are essential to understand the benefits of the bee species for regional food production.

The second line of activities concerning the bees of Carajás is the rescue of bee nests in areas where the native vegetation is being removed, authorised by the law of enterprise development. The support provided by the biological material compiled in the present volume will be crucial for identifying the rescued bee species, many of which are little known. It will form the foundation of new studies on bee diversity and bee products in the Amazon. Currently, species preselected for high honey production are used as matrices in a program on increasing the income of local communities.

References

- Camargo JMF, Pedro SRM (2013) Meliponini Lepeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version. Available at <http://www.moure.cria.org.br/catalogue>.
- Costa L (2019) Guia fotográfico de identificação de abelhas sem ferrão, para resgate em áreas de supressão florestal. Belém: Instituto Tecnológico Vale.
- Giannini TC, Costa, WF, Borges RC, Miranda L, Costa CPW, Saraiva AM, Imperatriz-Fonseca VL (2020) Climate change in the Eastern Amazon: crop-pollinator and occurrence-restricted bees are potentially more affected. *Regional Environmental Change* 20: 9.
- Moure JS, Urban D, Melo GAR (Orgs.) (2007) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. Curitiba: Sociedade Brasileira de Entomologia.

A detailed pencil sketch of a stingless bee on a tree trunk. The bee is positioned on the right side of the image, facing left. It has a large, dark, circular eye and a segmented body. The tree trunk is textured with fine lines and shading, suggesting bark. The background is a solid teal color. The text 'Stingless bees of Pará' is written in a white, serif font in the center of the image.

Stingless bees of Pará

Scientific collaboration between the Instituto Tecnológico Vale – Desenvolvimento Sustentável (ITV-DS) and the Coleção Entomológica “Prof. J. M. F. Camargo” enabled the retrieval of photographic material and the reorganization of this collection. The photographs of bees and nests shown below represent part of the holdings of Coleção Entomológica “Prof. J. M. F. Camargo”.

To facilitate your reading...

Trichotrigona extranea

species name

Camargo & Moure, 1983

Name(s) of the author(s) and year of publication



The scientific research that pursues the classification of biological diversity is called Taxonomy. The taxonomic practice involves the designation of some specimens representing each species to have a very special role. These specimens are called **types** and the set of type specimens is called a **type series**. In the process of describing a new species, scientists designate one or more specimens to compose the type series. This process guarantees confidence regarding the association between the scientific concept of species recognized by science and specimens preserved in scientific collections and archives. Type specimens such as *holotypes*, *paratypes*, and *paralectotypes* are therefore very relevant in the process of describing and interpreting the biological diversity.

Occurrence map



Origin and identification labels

F. do R. Darcã R. Negro
AM. Brasil-2, 4-VIII-1980

1st label: locality and date of collection

SA-20,64°47'W, 0°25'S
Camargo, MoZucoto leg

2nd label: geographical coordinates for the collection site and name of the collector(s)

HOLOTIPO
Trichotrigona extranea
Camargo & Moure

3rd label (for type specimen): holotype, paratype or paralectotype, species name and author(s) name. Different colours are used to indicate the type specimen

The number and shape of the labels may vary, but the key information is the location, date, collector(s) and the taxonomic identity of the specimen.

Genus

Aparatrigona Moure, 1951



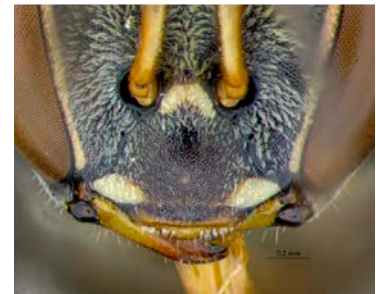
Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Moure JS (1994) Meliponini Neotropicais: os gêneros *Paratrigona* Schwarz, 1938 e *Aparatrigona* Moure, 1951 (Hymenoptera, Apidae). Arquivos de Zoologia 32: 33-109.

Aparatrigona impunctata (Ducke, 1916)

Common name:
mosquito-cupira.

Small bees (4.3 mm body length) that pollinate cupuaçu (*Theobroma grandiflorum*) and acapu (*Vouacapoua americana*) flowers and visit Brazil nut (*Bertholletia excelsa*) flowers.



Forte da Graça, rio Juruá
AM-Brasil. 02-06.08.1993
66° 6' W, 3° 39' S

Camargo, Pedro,
Mazucato, leg.



Colony within active termite nest in tarumã trunk, located at a height of 3 m. • Habitat: Old capoeira on terra firme • Carauari, Rio Juruá, AM • 23/07/1979



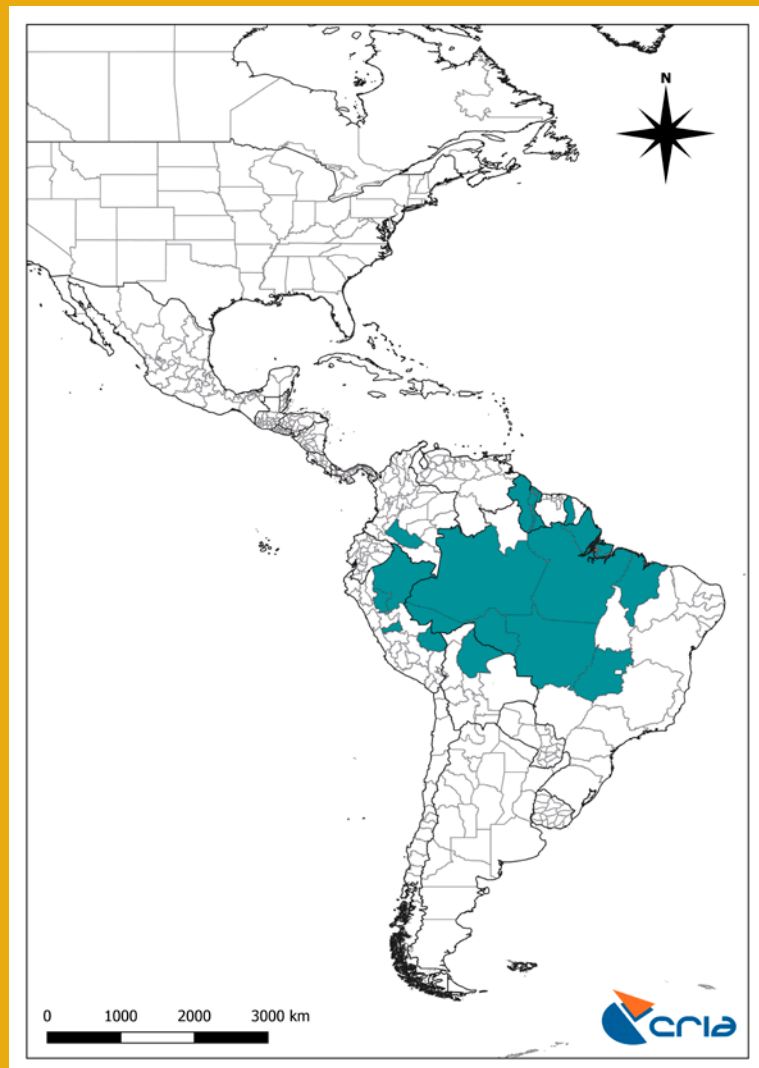
Small nest entrance, which allows the passage of only one bee at a time • Habitat: Old capoeira in terra firme, wood • Carauari, Rio Juruá, AM • 23/07/1979



The nest is housed inside an active termite nest in a pre-existing hollow and it is surrounded by a thin layer of involucrum. Brood cells are arranged into horizontal combs, and royal cells of much larger size are built at the margins of these combs. Honey and pollen are stored in egg-shaped pots.

Genus

Celetrigona Moure, 1950



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Pedro SRM (2009) Neotropical Meliponini: the genus *Celetrigona* Moure (Hymenoptera: Apidae, Apinae). Zootaxa 2155: 37-54.

Celetrigona longicornis (Friese, 1903)

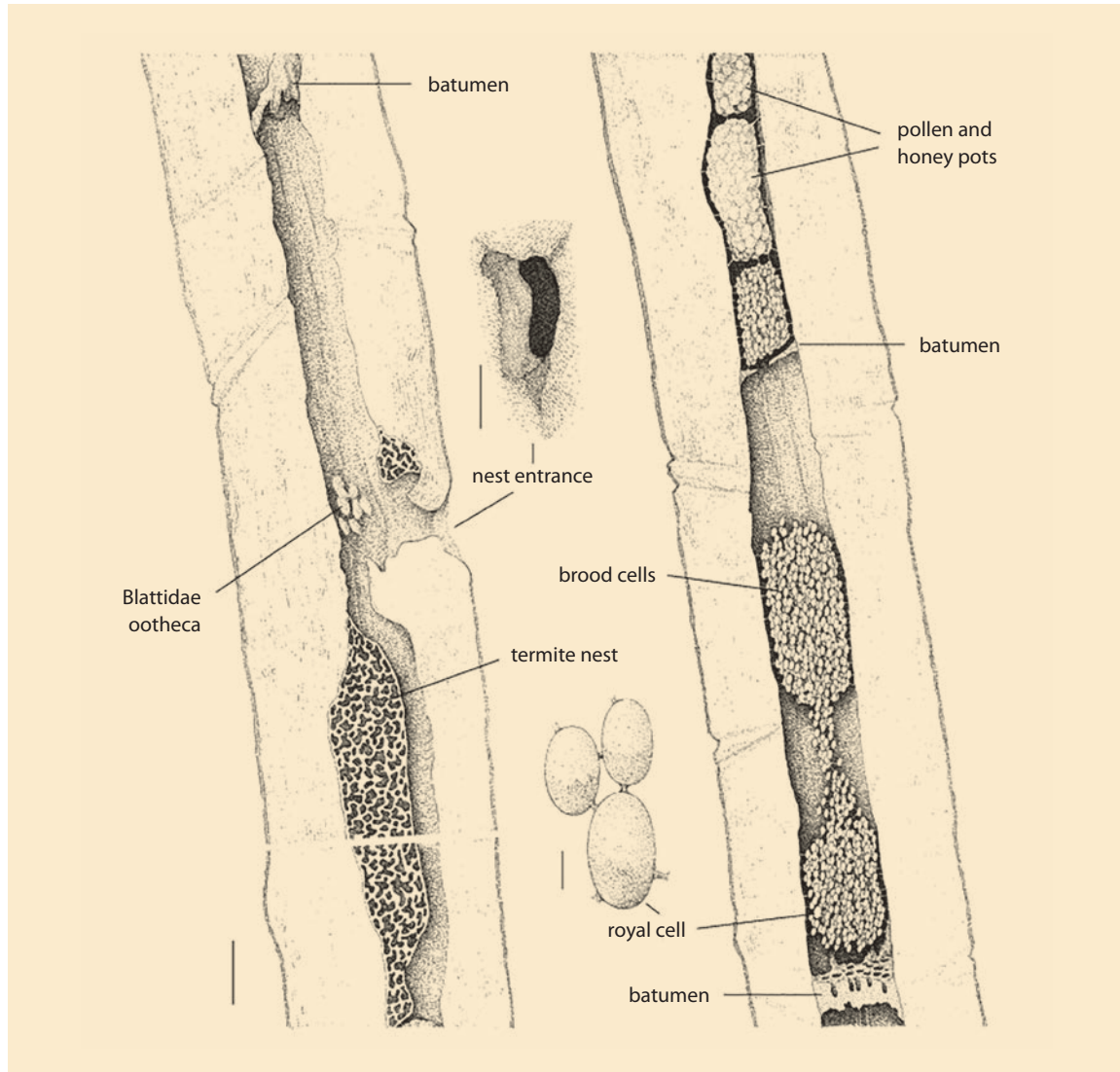
Common name: abelha-formiga.

This is a genus of small bees (3.5–4.3 mm body length).

Found in Carajás, PA.

Barra do Garças
MT. BRASIL
10.24.I. 1971
Col. Camargo
Celetrigona
longicornis
(Friese, 1903)
Det. Camargo 1977





Source: Camargo JMF, Pedro SRM (2009) Neotropical Meliponini: the genus *Celetrigona* Moure (Hymenoptera: Apidae, Apinae). Zootaxa 2155: 37-54.

Celetrigona manauara Camargo e Pedro, 2009

Worker body length is 3.4 mm. *Manauara* means born in Manaus.



Manaus - Boulevard
AM - Brasil - 1239
ninhod 14-IV-1986
M.V.B. Garcia

Celetrigona manauara
sp. n.
Camargo & Pedro, MS

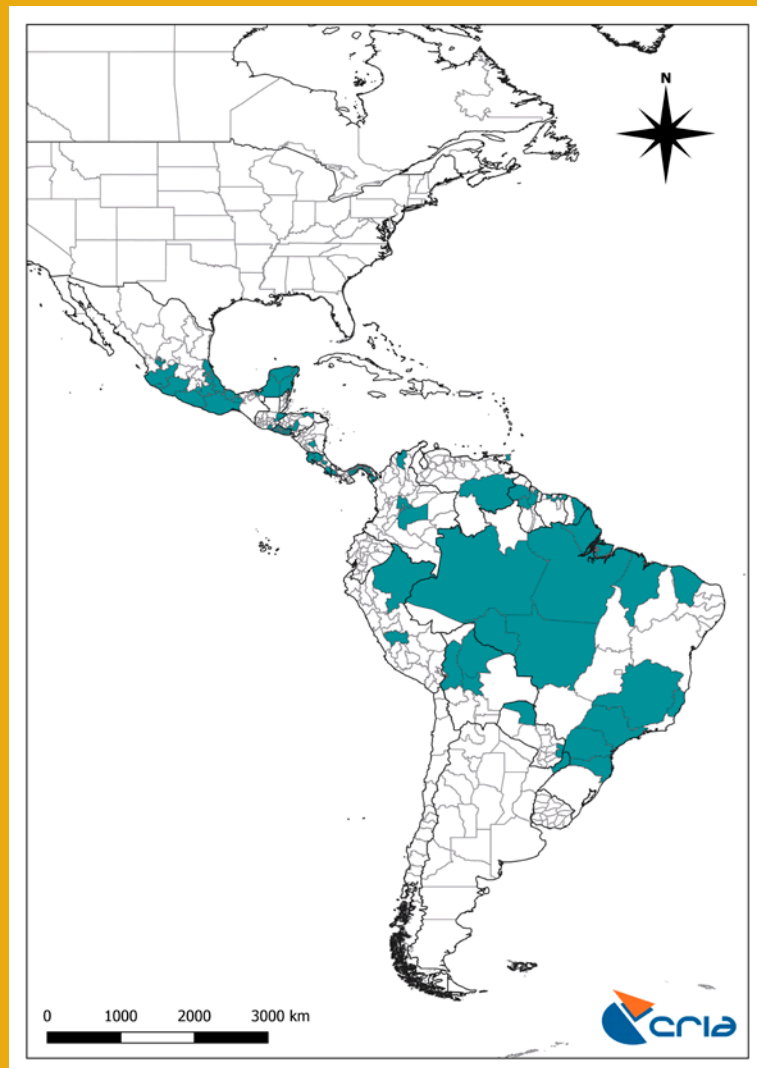
HOLOTYPE

(4)



Genus

Cephalotrigona Schwarz, 1940



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lepageletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Cephalotrigona capitata (Smith, 1854)

Common names: abelha papa-terra, mombucão, quare negra, mombuca, eiruzu, mergrito, eiruzu grande.

Has a wide geographical distribution. Its nests are found within live tree cavities, where large quantities of honey is stored. Medium-sized bees (8.6 mm body length) are very gentle. Pollinates annato (*Bixa orellana*) flowers and visits coffee (*Coffea arabica*) and sunflower (*Helianthus annuus*) flowers.



C. capitata
(Smith, 1854)
auctorum
Det. Camargo, 2008

Canavieiras-BR
Brasil. 25-V-1994
ALUC 1kg. of
mombuca n.v. 94/1476

Cephalotrigona femorata (Smith, 1854)

Common names: mombucão-da-Amazônia, língua de Einstein. Nests within hollow trees in terra firme forest. Nest entrance with a tongue-like projection. Large horizontal brood combs, nearly 22 cm in diameter. Medium-sized bees (10.3 mm body length). Visits Brazil nut (*Bertholletia excelsa*) flowers.



Cephalotrigona
capitata femorata
Smith, 1854
Det. Camargo 1990

Res. Br 124
25.3.16m 41
224.264(5159
43.404(N)

MANAUS, AM
PDRFE 1/18/89
R.L. OLIVEIRA

1900621

Genus

Dolichotrigona Moure, 1950



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Pedro SRM (2005) Meliponini Neotropicais: o gênero *Dolichotrigona* Moure (Hymenoptera, Apidae, Apinae). Revista Brasileira de Entomologia 49: 69-92.

Dolichotrigona longitarsis (Ducke, 1916)

Common name: lambe-olhos.

Workers are small (3.6 mm body length). When workers face predation at their nest, a cloud of defending bees attack, flying into the nose, ears and eyes. Other defensive mechanism includes caustic secretions left by dead workers, that cause irritation to the eyes.



RO-9643
BRASIL Rondônia
Porto Velho
Estação Ecológica Cuniã

22-Maio-1997
08°23'34.0"S-63°32'01.9"W
Brown, Boinã, Vieira
No.

**Dolichotrigona
longitarsis
(Ducke, 1916)
Det. Camargo, 2004**

Genus

Duckeola Moure, 1944



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Duckeola ghiliani (Spinola, 1853)

Medium-sized bees
(7–10 mm body length).
Although very gentle, it
is the only stingless bee
species that fights back
against the obligate robber
bee *Lestrimelitta*.



JANAUCA
Maués-AM

27

T. (Duckeola)
ghiliani
(Spinola)
Det. Camargo, 1976

BRASIL
XII - 1975
V.P. ANDRÉJOLES

Nest entrance with yellow resin. Nest within a hollow of a dry "cumari" trunk. • Habitat: *roçado* (traditional cultivated areas), *terra firme*, margin on the Maraã side • Maraã, Japurá River, AM • 18/08/1980



The nest occupied a hollow tree with 4 m in length and 10 cm in width. Generally, colonies are composed by thousands of workers. The brood area is large (65 cm in length and 10 cm in diameter) and is not surrounded by involucrum layers. Cerumen pillars are used as anchors of nest elements, extending to the cavity walls.

Nest within a hollow of a dry trunk • Habitat: Old *igapó*, *terra firme* margin, tall trees • Ponta do Gavião, Rio Negro, AM • 31/07/1999



Nest with many food pots, which can store more than 3 litres of honey. The mass-compacted food pots have twinned walls, and are composed by dark brown cerumen.

Brood cells are more or less spherical (10 mm in length and 7 mm in diameter) arranged into horizontal combs, regularly spaced by 5–10 mm.

Habitat: *Roçado*, *terra firme*, margin on the Maraã side • Maraã, Rio Japurá, AM • 18/08/1980

Genus

Frieseomelitta Ihering, 1912



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Frieseomelitta flavicornis (Fabricius, 1798)

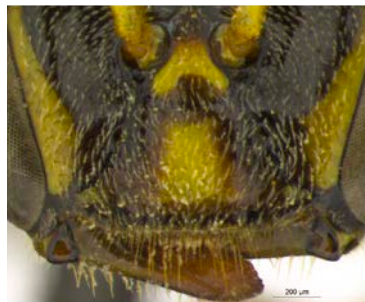
Common names:

marmelada amarela

mais mansa, branca.

Nests in live trees.

Visits tomato (*Solanum lycopersicum*) flowers.



FRENCH GUIANA: Cayenne
2.0 km W. 9 May 1982
D. Roubik coll. No. 57

Trigona
(Frieseomelitta)
savannensis
Roubik det. 82





Nest in a live tree cavity. • Habitat: *Terra firme* forest, *roçado* edge • São Jorge, Rio Negro, AM • 26/06/1999

Egg-shaped food pots (2.0 x 1.3 cm) removed from a nest within a live tree cavity. • Habitat: *Terra firme* forest, *roçado* edge • São Jorge, Rio Negro, AM • 26/06/1999



Frieseomelitta portoi (Friese, 1900)



UFMA

Sao Luis, MA, Brasil
5 -XII-1982
Camargo, MaZucato 821462

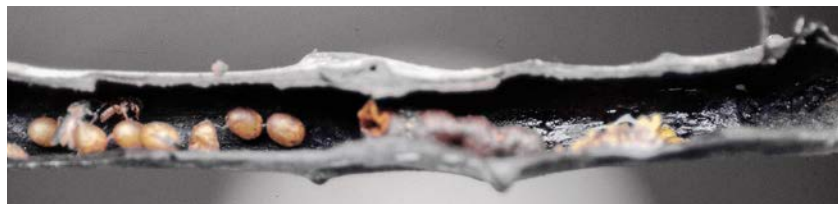
A single hollow in a dry embauba trunk houses three nests. Nest entrance with 2 mm in diameter. The bees are aggressive, flying fast and into the hair. •
Habitat: *Capoeira, terra firme*
• Igarapé-Açu, Rio Negro, AM 07/08/1999



Nest in a dry *cipó-ambé*. •
Habitat: *Igapó* forest, island bank • Santa Isabel do Rio Negro, AM • 12/07/1999



Clustered brood cells inside a nest in a very thin vine, with 1.8 cm in diameter.



Food pots inside the nest in a very thin vine.



Frieseomelitta trichocerata Moure, 1990

Medium-sized bees (6 mm body length). Establishes new nests in decomposing logs, in sunny locations, such as roçados, igapós and the margins of blackwater lakes. Visits Brazil nut (*Bertholletia excelsa*) flowers.



Frieseomelitta varia
Det. Moure-1970

Frieseomelitta varia varia
(Lep. 1936)
sensu Mémbr, 1950
Det. Camargo 1992

Porto Velho
Rorônia - Brasil
12-22° X - 1966
Col. Camargo

pelos longo
no escapo



Entrance of nest housed in a dead *marimari* tree cavity. • Habitat: *Igapó*, at the boundary with *terra firme* • Igapó Jaraqui, Rio Juruá, AM • 27/07/1993



Clustered brood cells • Habitat: Dense forest, lowlands, plateaus • Santa Maria do Boiaçu, RR • 19-20/08/1980

Genus

Geotrigona Moure, 1943



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Moure JS (1996) Meliponini Neotropicais: o gênero *Geotrigona* Moure, 1943 (Apinae, Apidae, Hymenoptera), com especial referência à filogenia e biogeografia. *Arquivos de Zoologia* 33: 95-161.

Geotrigona aequinoctialis (Ducke, 1925)

Common name: mombuca.
Body length is 5.0–5.4 mm and head width measures 2.44 mm. Body with bright colour.



UFMA

Sao Luis, MA, Brasil
21-III 1982
Mazucato, Camargo

Geotrigona
aequinoctialis
Ducke, 1925
Det. Camargo 1971

Geotrigona kwyrakai Camargo & Moure, 1996

Body length is 5.56 mm and head width measures 2.48 mm.



BRAZIL - Para
Jacarecanga
October 1959
(M. Alvarenga

PARATYPE
Geotrigona
subgrisea
kwyrakai
Moure &
Camargo, 1996

Geotrigona mattogrossensis (Ducke, 1925)

Body length is 5.2 mm and head width measures 2.32–2.56 mm, in specimens collected in Muçum, PA (labels mention Mussum), near the Rio Tapajós.



Mussum - Rio Tapajós
PA - Brasil

151c(T-37)

SA-21,55°25'W;3°40'S
24,28-I-1979. Camargo

Geotrigona *mattogrossensis*
(Ducke, 1925)
Det. Moure 1991



Timid bees that do not attack the observer.

In the immediate vicinity of *G. mattogrossensis* nest, either termite or ant nests were absent. The stingless bee nest was surrounded by a multilayered black involucrum. Thinner layers of involucrum involved the brood area, composed by 14 spiral combs (the largest comb was 8 cm in diameter). Honey pots measured 7.0–9.0 cm in height and 1.7 cm in diameter.

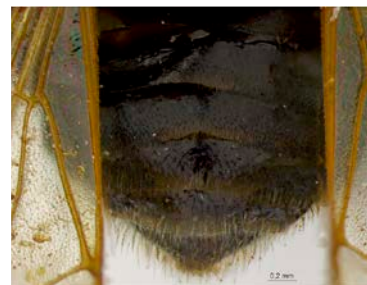
Underground nest • Habitat: Terrace forests, Brazil nut stand • Mussum, 15 km S Aveiro, PA • 24-28/01/1979



Geotrigona mombuca (Smith, 1863)

Common names: guira, guiruçu, iruçu-mineiro.

Body length is 5.4 mm and head width measures 2.48 mm. Timid bees that do not attack the observer. Nests are underground. Visits cotton (*Gossypium hirsutum*) flowers.



nº 33
col. 2

Ribeirão Preto SP
XI, 1983
Lacerda, L. M. leg

PARATYPE
Geotrigona
invisitata
Moura &
Carniero, 1991

Geotrigona
mombuca (Sm.)
com paratipo
com o tipo
Det. Comarço, 1995

Geotrigona subnigra (Schwarz, 1940)

Body length is 5.23 mm and head width measures 2.36 mm. Nesting habits are unknown.



LAGO AGUA FRIA, PA.
Rio Trombetas - BRASIL

SA.21-X-C,56°51'W,1°25'S
13-15,II-1979. Camargo

Geotrigona
subnigra
Schw., 1940
Det. Moure, 1944

comparado com
o holótipo
Acc. 36159
AMNH
Det. Camargo, 1995

Genus

Lestrimelitta Friese, 1903



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Marchi P, Melo GAR (2006) Revisão taxonômica das espécies brasileiras de abelhas do gênero *Lestrimelitta* Friese (Hymenoptera, Apidae, Meliponina). Revista Brasileira de Entomologia 50: 6-30.

Lestrimelitta monodonta Camargo & Moure, 1989

Common name: limão.

Body length is 6.08 mm and head width measures 2.16 mm. Workers produce a strong lemon-like odour (citral), when they attack nests of other stingless bee species. During attack, this odour causes retreat of host species and *L. limao* successfully conquer the nests.



Ilha de Maracá - RR
Brasil 5-10/10/1987
Lucio A.O. Campos
Marcos V. B. Garcia

HOLOTYPE
Lestrimelitta
monodonta
Camargo &
Moure, 1989



Nest within a hollow tree • Habitat: Tall *terra firme* forest • Ponta do Gavião, Rio Negro, AM • 30/07/1999

Lestrimelitta rufa (Friese, 1903)

Body length is 7.05 mm and head width measures 2.3 mm.



Ecuador Pasta
2a - Puyo
VIII-86
Legit: E. O'DONC

Lestrimelitta rufa
(Friese, 1903)
Det. Camargo, 2005

Lestrimelitta rufipes (Friese, 1903)

Common names: limão, iraxim.

Body length is 7.25 mm and head width measures 2.28 mm. Nests within living trees that sometimes are shared with other stingless bee species.



Barro do Garças
MT. BRASIL

10.24.I.1971
Col. Camargo

Lestrimelitta
limão
(Smith, 1863)
Det. Camargo 1977

Lestrimelitta rufipes
(Friese 1903)
Det. Camargo, 2005

Lestrimelitta rufipes

Nest entrance in a live tree cavity. • Habitat: Cerrado, *vereda* margin
• Mateiros, TO • 10-12/07/1995



Nest within a hollow tree
• Habitat: Dense forest, lowlands, plateaus • Acanga, Rio Negro, AM • 06-08/08/1980

Genus

Leurotrigona Moure, 1950

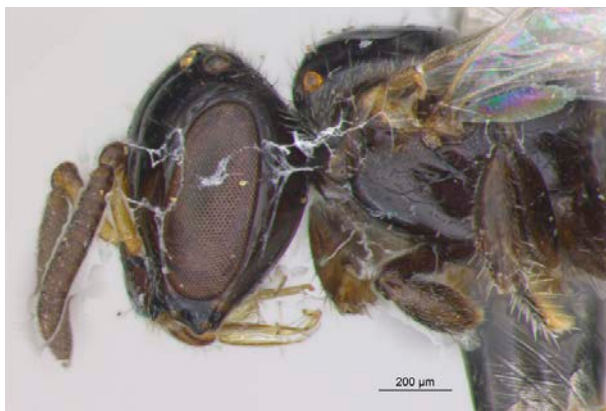


Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Leurotrigona pusilla Moure & Camargo, 1988

Common name:
lábios de morena.

Its nests are found in small cavities built by Cerambycinae beetles, and by termites in dry wood, wooden poles and building walls. Pollinates cupuaçu (*Theobroma grandiflorum*) flowers.



*Leurotrigona
pusilla* Camargo
& Moure, 1988
HOLOTYPE

marg.esq.do R.Negro

SA-19,66°49'W,0°13'S
Camargo MoZucato Iea

FoZ do Rio Curicuriari - AM,
R.Negro-Brasil-15,21-VII-80

230°C

Nest within a building wall • Habitat: Forest, sub-montane, dissected relief • Mouth of the Rio Curicuriari, AM • 15-21/07/1980



Genus

Melipona Illiger, 1806



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

(In this map, the geographic distribution of the genus *Melipona* corresponds to countries – not states or provinces, as shown for other stingless bee genera in this work)

Melipona (Eomelipona) amazonica Schulz, 1905

Among the species of the genus *Melipona*, this is considered one of the smallest bees. Nests in pequi tree (*Caryocar* sp.) cavities. Visits açai (*Euterpe oleracea*) flowers.



Porto Velho
Rondonia - Brasil
12 - 22 - X - 1966
Col. Camargo

M. marginata
amazonica Schulz
Det. Camargo 1977

Melipona (Eomelipona) bradleyi Schwarz, 1932



BRASIL Amazonas
S.Gabriel Cachoeira
Morro 6 Lagos
28.ix-6 x.199

300m
Arm Malaise
J.A.Rafael
J.Vidal

Melipona marginata
bradleyi
Schwarz, 1932
Det. S.Pedro, 1995

Melipona (Eomelipona) illustris Schwarz, 1932



Nogueiras, lago de Tefé
AM-Brasil, 25-26.08.1993
64° 48' W, 3° 19' S

Mp illustris
Schwarz, 1932
Det. Camargo, 1999

Camargo, Pedro,
Mazucato, leg.

Melipona (Eomelipona) ogilviei Schwarz, 1932



Ilha de Maracá - RR
Brasil 5-10/10/1987
Lucio A. O. Campos
Marco V. B. Garcia

Melipona ogilviei
Schwarz, 1932
Det. Camargo 1987

Melipona (Eomelipona) ogilviei



Nest within a hollow tree •
Habitat: Dense floodplain
forest and flattened relief •
Tauri, PA • 29/01/1979



Melipona (Eomelipona) puncticollis Friese, 1902

Common name:
uruçu-amarela-
preguiçosa.



FRENCH GUIANA: Kourou
15.5 kmsw 24 May 1981
D. Roubik No. 33

M. puncticollis
Friese, 1902
Det. Camargo, 1999

Melipona (Eomelipona) schwarzi Moure, 1963



TEFF Am. Br.
1-4-XII 61
F. M. Oliveira.

PARATYPE
Melipona
schwarzi
J. S. Moure 1963





Nest within a hollow tree •
Habitat: *Igapó* forest, tall forest, shaded • Ponta do Gavião, Rio Negro, AM • 30/07/1999



Melipona (Melikerria) fasciculata Smith, 1854

Common names: tiúba, tiúba-grande, jandaíra-preta-da-amazônia, ngái-re.

Pollinates cassava (*Manihot esculenta*) flowers, camu-camu (*Myrciaria dubia*), bell pepper (*Capsicum annuum*), habanero type pepper (*Capsicum chinense*), tomato (*Solanum lycopersicum*), eggplant (*Solanum melongena*), açaí (*Euterpe oleracea*), annato (*Bixa orellana*) and yellow mombin (*Spondias mombin*).



São Caetano
de Odivelas
PA - Brasil

M. compressipes
fasciculata
Sm. 1854
Det. Camarao 1979

Melipona (Melikerria) fasciculata



Nest within a pequi tree
(*Caryocar brasiliense*,
Caryocaraceae) cavity •
Habitat: Open cerrado •
Krahó Reserve, Galheiros, TO
• 18/01/1993



Melipona (Melikerria) interrupta Latreille, 1811

Common names: jandaíra-preta-da-amazônia, jupará. Important species for stingless beekeeping, due to its high honey production and optimized management practices. Visits cotton (*Gossypium hirsutum*) flowers.



VENEZUELA: Zulia, El Tucuco (51 Km. S.O. de Machiques).
TV- 1984

MALUZ
HYM
385

Colectores:
E. Inoiarte
E. Rubio E.
T. Borrego

M. interrupta
Latr.: 1811
Det. Camargo, 2008

Melipona (Melikerria) interrupta



Nest within a hollow tree; perforated batumen
• Habitat: Floodplain • Santa Maria, Itaituba, PA
• 18-20/01/1977



Melipona (Michmelia) flavolineata Friese, 1900

Common names: uruçú-amarela, ira-açu, ngái-kumrenx, mehn-krak-krak-ti.

Due to the production of highly appreciated honey, this is one of the most important species for stingless beekeeping in Pará State. Visits açai (*Euterpe oleracea*), yellow mombin (*Spondias mombin*) and eggplant (*Solanum melongena*) flowers.



W.E.KERR
830625

SAO LUIS, MA
Brasil. 7.V.1983

Melipona pubiventris
flavolineata
Friese, 1900
Det. Camargo 1991



Melipona (Michmelia) fuliginosa Lepelletier, 1836



Common names:
uruçu, turucu,
mandury-preto,
erereú-negra, mel-de-
anta, tapii-ei, tapieira.
This species does not
adapt well to wooden
hives. By pillaging
nests of other
stingless bee species,
M. fuliginosa can also
obtain food.



BRASIL
Rondonia
Costa Marques

M. (Michmelia) fuliginosa
Lepelletier, 1836
Det. Camargo, 2007

3250 - 18/11/96
S12°19'46"
W64°14'39"
Brown, Boina, Vieira

Melipona (Michmelia) fuliginosa



Nest within a live tree cavity •
Habitat: *Terra firme* forest, Brazil
nut stand, shaded tall forest •
Tapera, Caurés, Rio Negro, AM •
27/07/1999



Melipona (Michmelia) fulva Lepeletier, 1836



Rio Urucuaá
Amapá Territory
Brazil
Coll. W. E. Kerr

Colony No. 245
R. Nogueira Neto

Melipona fasciata
pseudocentris CKH.
Det. by H. F. Schwarz

Melipona fulva
Lepeletier, 1836
Det. Camargo 1991

Melipona (Michmelia) fulva

Nest within a hollow tree

- Habitat: Dense forest, plateau
- Lago Carimum, PA
- 16-17/02/1979



Melipona (Michmelia) lateralis

Erichson, 1848

Visits Brazil
nut (*Bertholletia
excelsa*) flowers.



FRENCH GUIANA
Sail, Mt. Galbao summit, 740 m
3°37' 18" N, 53°16' 42" W
6 JUN 1997; J. Asha, R. Brooks
FGJAB97-157

SNQ103061
KUNHM-ENT

Melipona lateralis
Erichson, 1848
Det. Carargo, 1998

Melipona (Michmelia) lateralis



Nest within yellow mombin tree cavity • Habitat: Transitional forest • Catrimani, Rio Branco, RR • 18/08/1980



Melipona (Michmelia) melanoventer Schwarz, 1932

Common name:
menhirê-udjà.
Visits eggplant
(*Solanum melongena*)
and annato (*Bixa*
orellana) flowers.



Pelem, Para,
Brazil,
Warwick E. Kerr

Melipona ♀
fasciata subsp.
melanoventer.
Schwarz ♀
Det. H. F. Schwarz

Melipona (Michmelia) nebulosa Camargo, 1988



1

Cuiabá, Santarém
Km. 2027-PA-Brasil

próximo Rio
Yamaxim-1977
Julistini leg.

HOLOTYPE
Melipona
nebulosa
Camargo, 1985



Nest within a live *puleiro de pato* tree cavity, at 9 m above the ground
• Habitat: *Igapó* forest, shaded • Grate Forte, Rio Juruá, AM • 08/08/1993



Melipona (Michmelia) paraensis Ducke, 1916

Common names: uruçú-boca-de-ralo, i-tekere.

Visits acerola (*Malpighia punicifolia*) flowers.



Orepoque - AP
Brasil - VI-59
F. V. Rodrigues

Melipona rufiventris
paraensis
Ducke, 1916
Det. Camargo 1991

M. paraensis
Ducke, 1916
comparado com
o tipo, 3.06.04
Det. Camargo, 2004



Nest within a hollow tree •
Habitat: *Terra firme* forest,
Brazil nut stand • Maraã, Rio
Japurá, AM • 19/08/1993



Nest within a hollow tree •
Habitat: *Igapó* forest • Ponta
do Gavião, Rio Negro, AM •
30/07/1999

Melipona (Michmelia) seminigra Friese, 1903

Visits yellow mombin (*Spondias mombin*) and eggplant (*Solanum melongena*) flowers.



Rio Trairão. PA – Brasil
(50 km NE Gradaús)

SB-22, 51°49' W, 7°21' S
21, 24-VII-79. Mazucato

Melipona seminigra
Peralígra
Mourelle & Kerr, 1950
Det. Camarao 1991

M. seminigra seminigra
Friese, 1903 • Nest
entrance in an *envirola* tree
cavity • Habitat: Dense
forest, lowlands • Igapó
Castanho, Rio Branco, RR •
21/08/1980



M. seminigra seminigra
Friese, 1903 • Nest entrance
in a live *mapatirana* tree
cavity • Habitat: *Terra firme*
forest • Marãã, Rio Japurá,
AM • 18/08/1993



M. seminigra abunensis
Cockerell, 1912 • Nest
entrance in a live *itaubarana*
tree cavity at 4 m above the
water level • Habitat: *Igapó*
(lago Jacaré) • Arimã, Purus,
AM • 08/02/1986

Melipona (Michmelia) seminigra



M. seminigra pernigra Moure & Kerr, 1950 • Nest within a hollow tree, at 4 m above the ground • Habitat: *Várzea* forest, margin of the Rio Fresco • Gotire, PA • 05-20/08/1983



M. seminigra seminigra Friese, 1903 • Nest within an *envirola* tree cavity • Habitat: Dense forest, lowlands, plateaus • Santa Maria do Boiaçu, RR • 19-20/08/1980



M. seminigra seminigra Friese, 1903 • Nest within a live *capurana* tree cavity • Habitat: *Igapó* forest • Lago Uará, Rio Solimões, AM • 12/08/1993

Genus

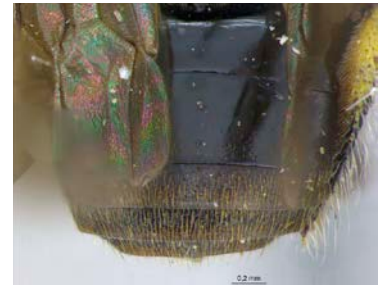
Nannotrigona Cockerell, 1922



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

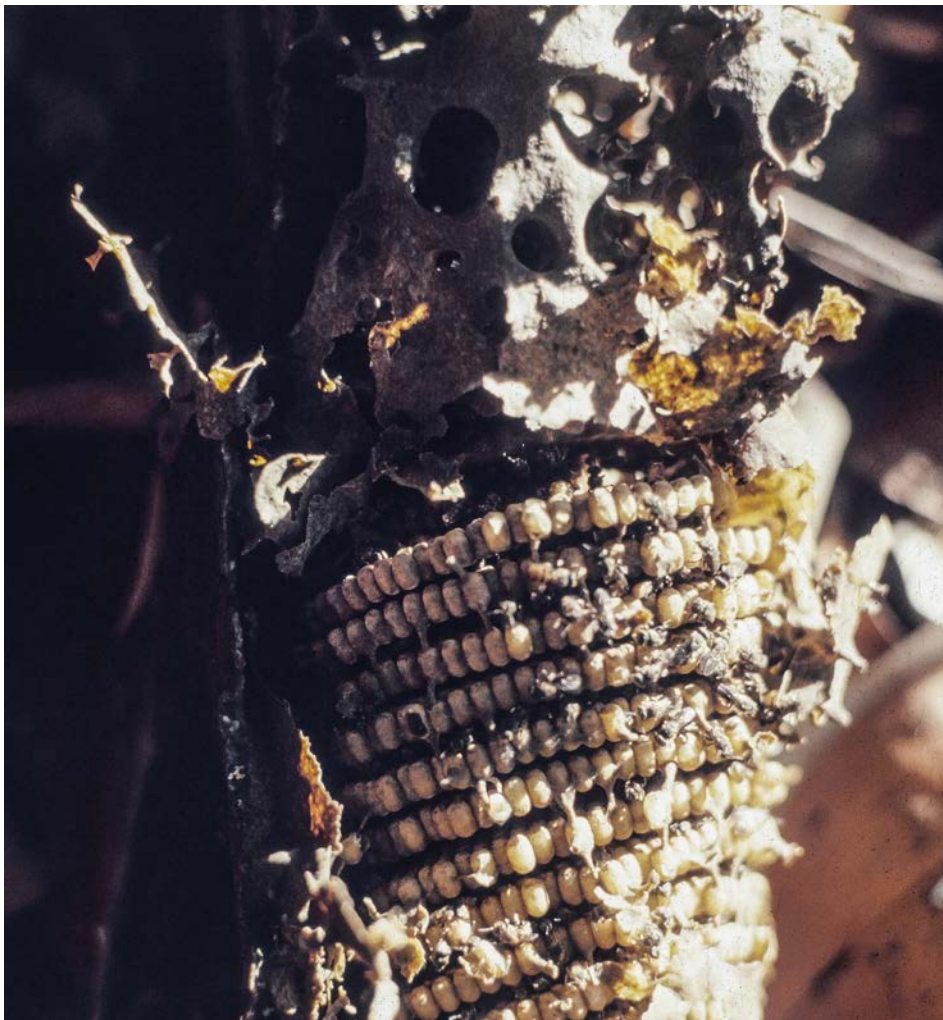
Rasmussen C, Gonzalez VH (2017) The neotropical stingless bee genus *Nannotrigona* Cockerell (Hymenoptera: Apidae: Meliponini): An illustrated key, notes on the types, and designation of lectotypes. *Zootaxa* 4299: 191-220.

Nannotrigona minuta (Lepeletier, 1836)



SAO LUIS, MA
Brasil, 30. XII.
1982
MaZucato, Aily
802860

Nest within a hollow tree • Habitat:
Cerrado enclave • Alter do Chão,
PA • 03-04/02/1979



Nest within a
hollow tree •
Habitat: Cerrado
enclave • Alter
do Chão, PA •
03-04/02/1979

Nannotrigona punctata (Smith, 1854)

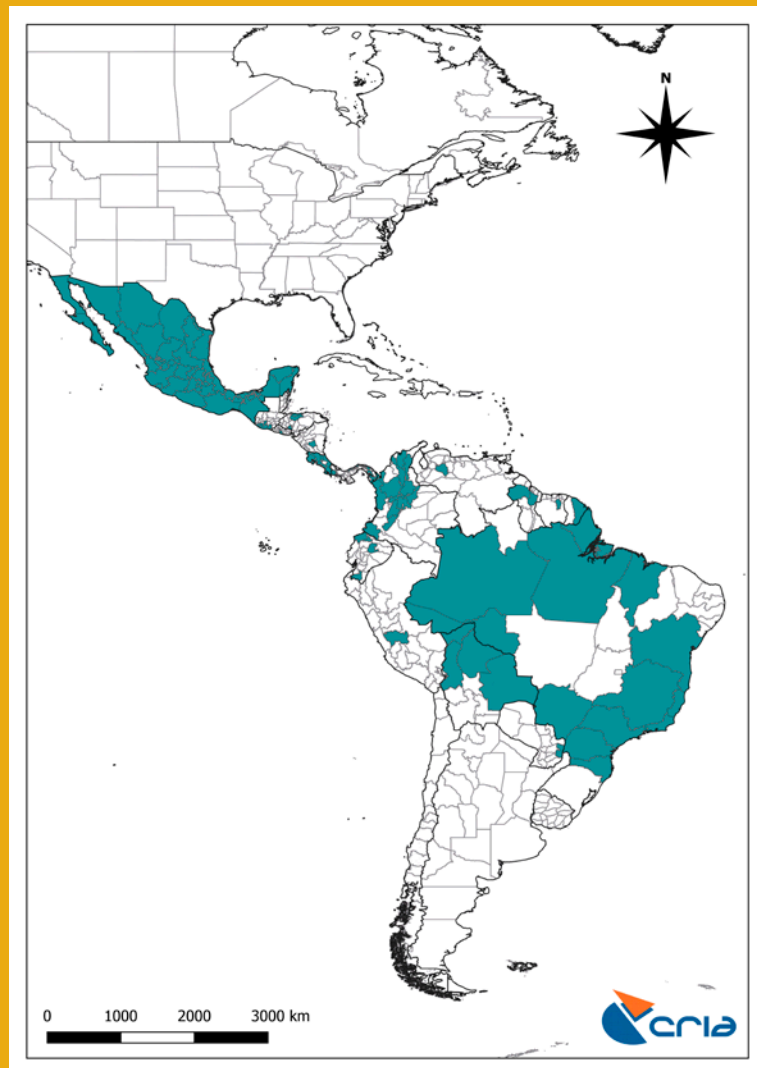
Visits murici (*Byrsonima crassifolia*), guava (*Psidium guajava*) and rambutan (*Nephelium lappaceum*) flowers.



FRENCH GUIANA: Sinnamary
15 km SE; palm planta-
tion rd. * 5 May 1982
D. Roubik coll No. 64

Genus

Oxytrigona Cockerell, 1917



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF (1984) Notas sobre o gênero *Oxytrigona* (Meliponinae, Apidae, Hymenoptera). Boletim do Museu Paraense Emílio Goeldi 1: 115-124.

Oxytrigona ignis Camargo, 1984



SB-22,51°49'W,7°21'S
21,24-VII-79. Mazucato

*Oxytrigona
ignis*
Camargo, 1983
HOLOTYPE

Rio Trairão. PA – Brasil
(50 km NE Gradaús)

Oxytrigona obscura (Friese, 1900)

Common name:
sicaé-negra.



FRENCH GUIANA: Sinnamary
15 km SW; ORSTOM station
Road May 2 1982
D. Roubik coll. No. 62

*Oxytrigona
obscura*
(Friese, 1900)
Det. Camargo, 2000

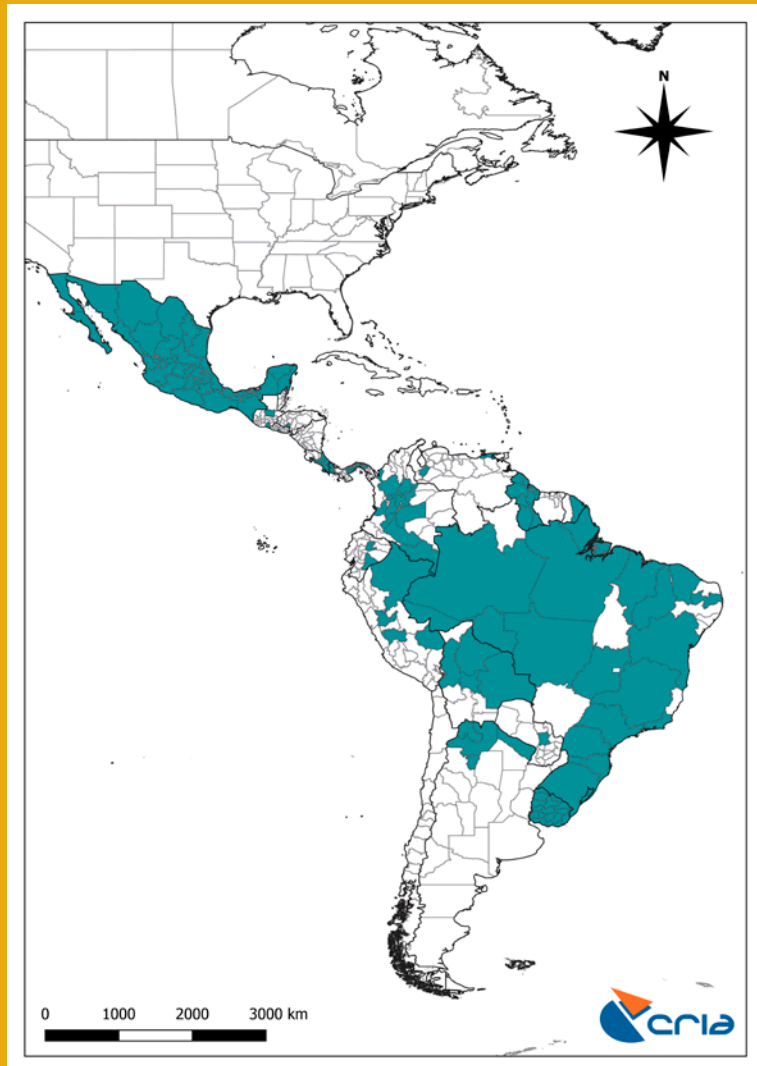
Oxytrigona obscura



Nest within a live tree cavity, at 10 m above the ground • Habitat: Tall forest, *terra firme* • Forte da Graça, Rio Juruá, AM • 05/08/1993

Genus

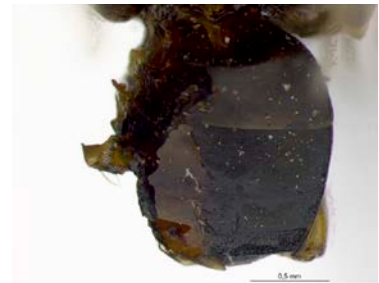
Paratrigona Schwarz, 1938



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Moure JS (1994) Meliponini Neotropicais: os gêneros *Paratrigona* Schwarz, 1938 e *Aparatrigona* Moure, 1951 (Hymenoptera, Apidae). Arquivos de Zoologia 32: 33-109.

Paratrigona crassicornis Camargo & Moure, 1994



MOCAJUBA PARÁ
BRASIL ♀ 1-1953
Orlando Rego

PARATYPE
Paratrigona
crassicornis
Camargo &
Moure, 1990



Paratrigona haeckeli (Friese, 1900)



BRASIL
Rorônia
Nova Mamoré

311 - 12/09/96
S10°19.440'
W64°46.775'
Brown, Boia, Vieira

*Paratrigona
haeckeli*
(Friese, 1900)
Det. Camargo, 1999

Paratrigona lineata (Lepeletier, 1836)

Common name:

jataí-da-terra.

Visits cotton (*Gossypium hirsutum*), sunflower (*Helianthus annuus*) and tomato (*Solanum lycopersicum*) flowers.



PASSOS - MG
Brasil 19.24 III-62
Claudionor Elias

*P. (Paratrigona)
lineata*
Det. Moure - 1966



Paratrigona lineatifrons (Schwarz, 1938)



F. do R. Dará R. Negro
AM. Brasil-2.4-VIII-1980

SA-20,64°47' W, 0°25' S
Camargo, MaZucato leg

Paratrigona
lineatifrons
(Schwarz, 1938)
Det. Camargo 1980

Paratrigona lineatifrons

Nest entrance



Nest within an arboreal termite nest
• Habitat: Dense forest, transitional area, undulated relief • Mouth of the Rio Daraá, AM • 02-04/08/1980



Paratrigona pannosa Moure, 1989



Serra do Navio-AP
Brasil • 7-II-62
F. M. Oliveira

celtrig
(Spinola, 1853)
Det. Moure-1966

Paratrigona
pannosa
Moure, 1989
Det. Moure 1980

Paratrigona prosopiformis (Gribodo, 1893)



Vila Nova do Tonantins
AM, Brasil. SA-19.68-3f. IX

22, 23-I-1977, Camargo
M. Mazucato leg.

P. (Paratrigona)
prosopiformis
(Gribodo, 1893)
Det. Camargo 1977

Genus

Partamona Schwarz, 1939



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lepeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Pedro SRM, Camargo JMF (2003) Meliponini neotropicais: o gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae). *Revista Brasileira de Entomologia* 47: 1-117.

Partamona ailyae Camargo, 1980



COLEÇÃO
CAMPOS SEABRA

DZUFP

TEFÉ
Amazonas Brasil
IX-1959
R. Carvalho

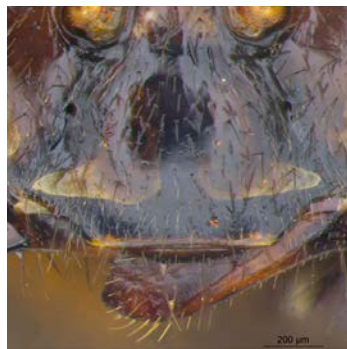
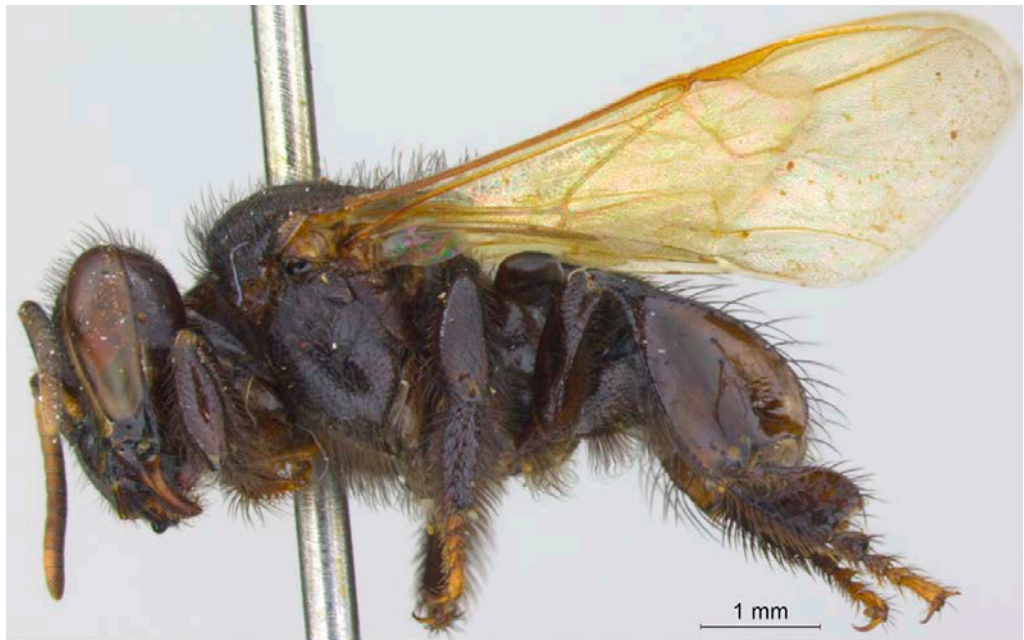
Partamona ailyae
Camargo, 1980
Det. S. Pedro, 1996



Nest within an active termite nest in dry, rotten trunk
 • Habitat: *Terra firme* forest – at 30 to 40 m above the ground
 • Maraã, Rio Japurá, AM • 17/08/1993

Nests: in a termite nest in a rotten trunk (A); in a trunk of a live Brazil nut tree (B); under tree trunk (underground nest) (C); above the ground (D).
 Source: Camargo JMF, Pedro SRM (2003) *Meliponini Neotropicais: O gênero Partamona Schwarz, 1939* (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. *Revista Brasileira de Entomologia* 47: 311-372.

Partamona auripennis Pedro & Camargo, 2003



168c (♂T-54)

GENÉTICA
F.M.R.PRETO

TAUARI, PA.
Rio TAPAJÓS Brasil
SA.21-55°7'W;3°5'S
29-I,1-II-79.Camargo

HOLOTYPE
Partamona
auripennis Pedro
& Camargo, 1988



Nest within an abandoned arboreal termite nest (in an *igarapé* [typical watercourse of the Amazon region]) •
Habitat: Dense floodplain forest and flattened relief •
Tauri, PA • 01-01/29/1979



Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.

Partamona chapadicola Pedro & Camargo, 2003

Common name:
boca-de-barro.



665c

39 Km S Chapadinha
MA, 43°30' W, 5°5' S
Brasil, 12-13/IX/1994
Camargo, Pedro leg.

HOLOTYPE

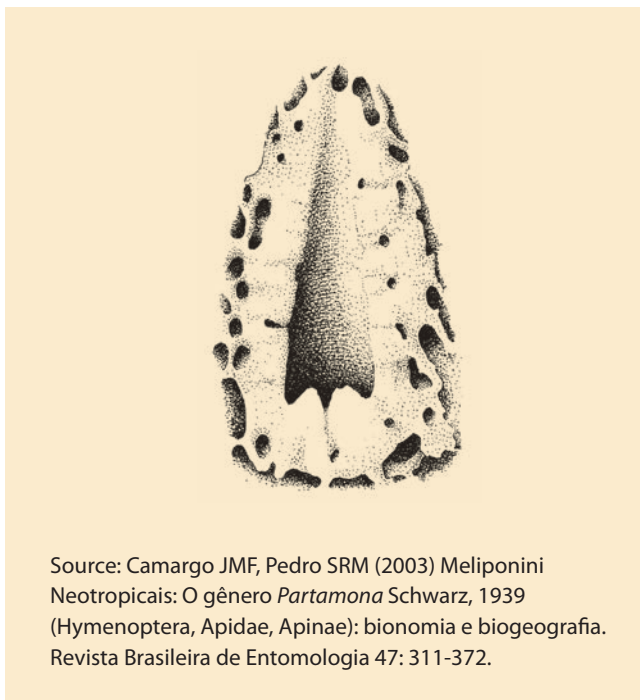
HOLOTYPE
Partamona
chapadicola Pedro
& Camargo, 1988

Partamona chapadicola



Nest entrance in a hollow tree (possibly along with a termite nest) • Habitat: Cerrado, plateau
• Chapadinha, 39 km, MA • 13/11/1994

Nest entrance at the base of live tree trunk, at 50 cm above the ground • Habitat: Open cerrado • Krahó Reserve, Galheiros, TO • 18/01/1993



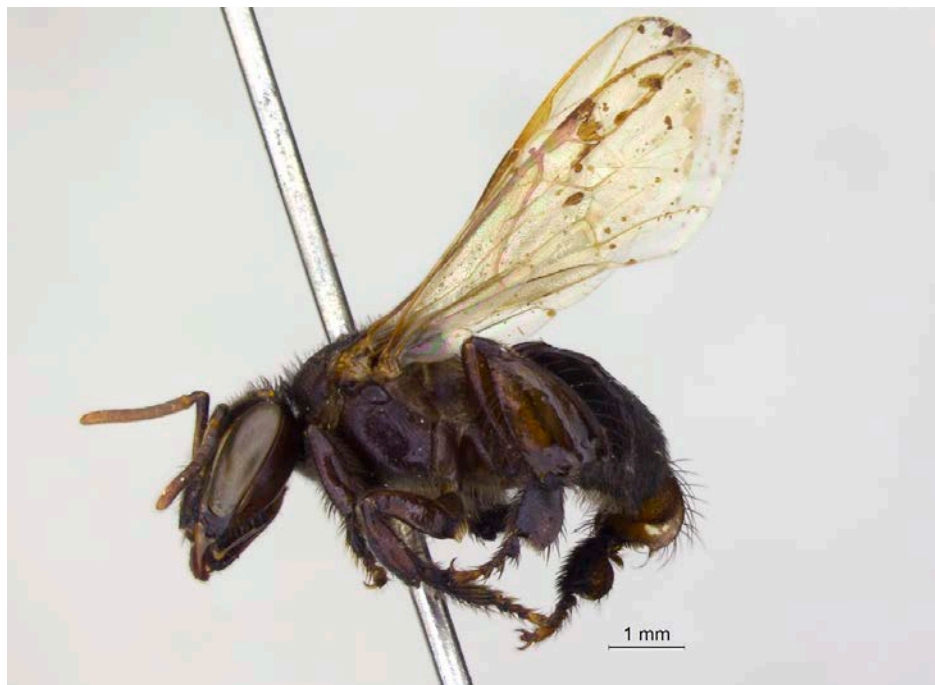
Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.



Partamona combinata Pedro & Camargo, 2003

Common names:
ngài-kàk-ny, myre-ti,
hasi-mane-bakuki.

Visits cucurbit (*Cucurbita*
spp.) flowers.



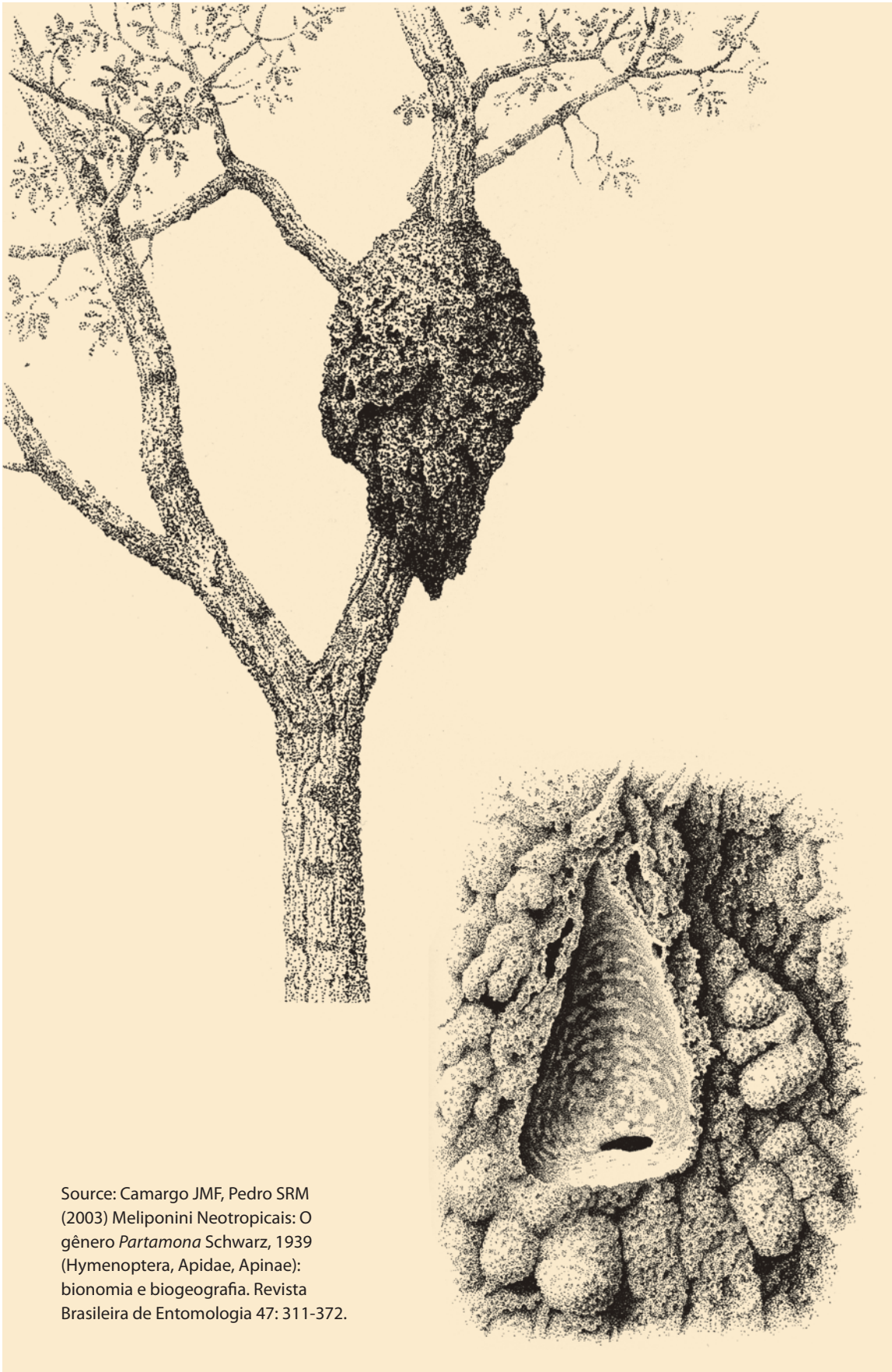
4c

HOLOTYPE

GENÉTICA
FM. R. PRETO

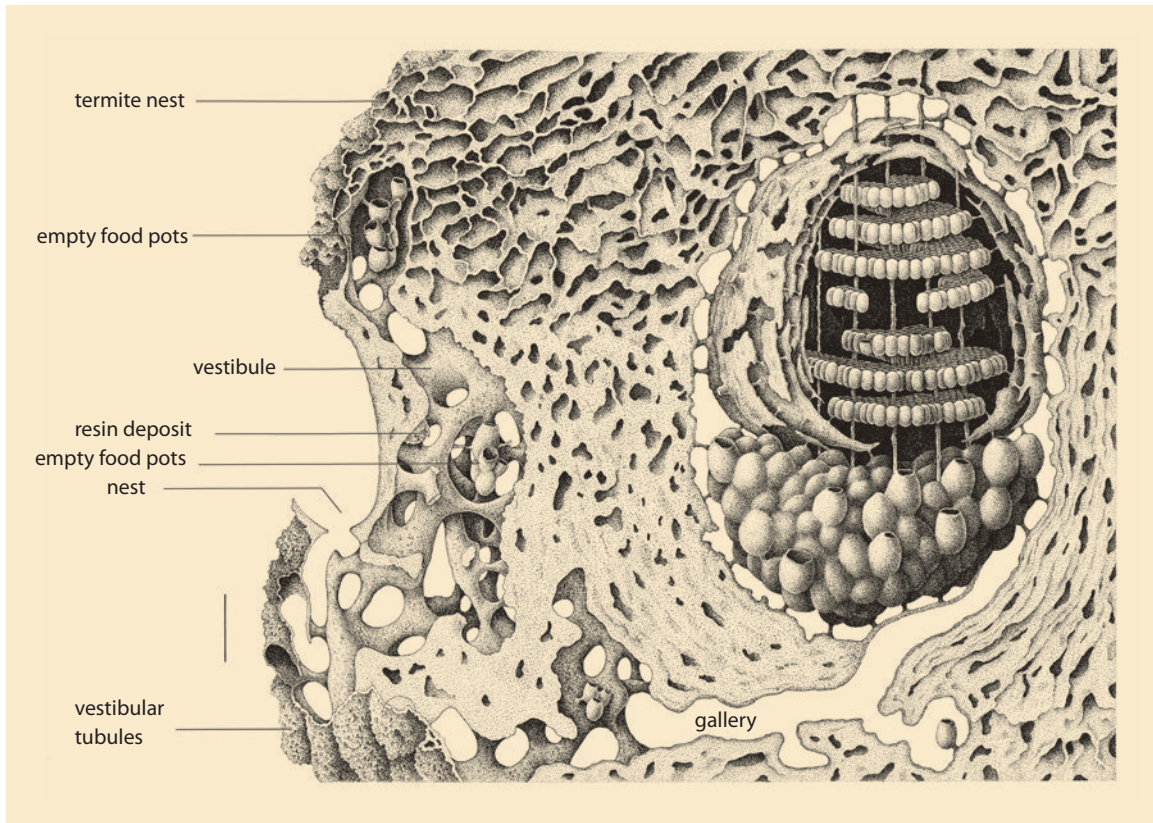
HOLOTYPE
Partamona
combinata Pedro
& Camargo, 1988

Barra do Garças
MT. BRASIL
10.24.I. 1971
Col. W.E. Kerr



Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.

Partamona combinata



Source: Camargo JMF,
Pedro SRM (2003)
Meliponini Neotropicais:
O gênero *Partamona*
Schwarz, 1939
(Hymenoptera, Apidae,
Apinae): bionomia e
biogeografia. Revista
Brasileira de Entomologia
47: 311-372.

Nest within an active
arboreal termite nest, at
2 m above the ground
• Habitat: Gallery forest
edge, at the border with
the cerrado • Krahó
Reserve, Galheiros, TO •
21/01/1993

Partamona ferreirai Pedro & Camargo, 2003



GENÉTICA
F.M. RIBEIRO

183c (:T-69)

L A G O A G U A F R I A , P A .
Rio Trombetas - BRASIL
SA.21-X-C,56°51'W,1°25'S
13-15,II-1979. Camargo

HOLOTYPE

HOLOTYPE
*Partamona
ferreirai* Pedro
& Camargo, 1973

Partamona ferreirai



Nest within an active termite nest in a hollow tree • Habitat: Dense forest, transitional area, undulated relief • Mouth of the Rio Daraá, AM • 02-04/08/1980



Nest within a termite nest fixed to a trunk • Habitat: *Igapó* forest, riverbank • Nazaré, Rio Negro, AM • 16/07/1999

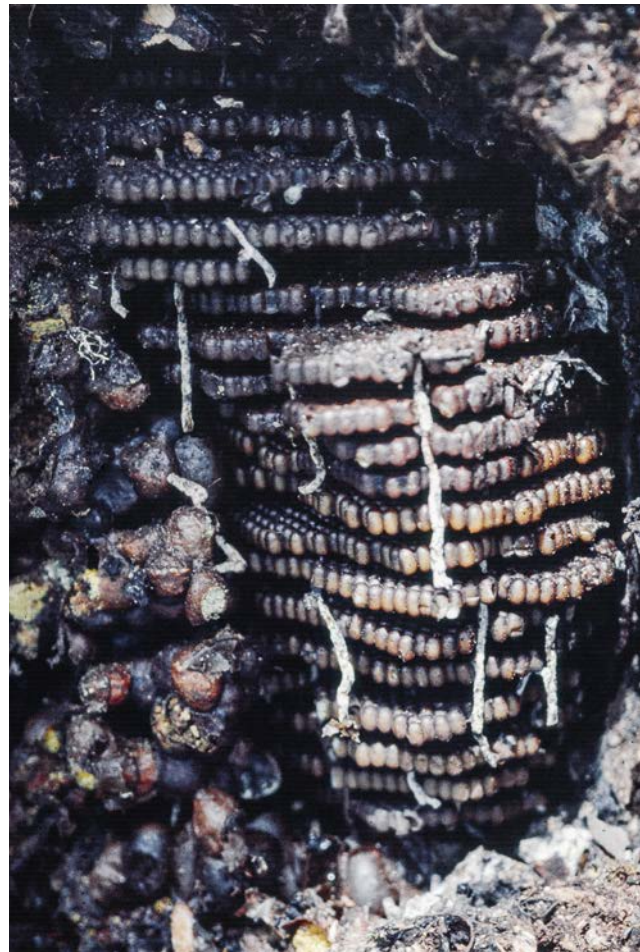


Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.



Nest within a termite nest fixed to a trunk • Habitat: *Igapó* forest, riverbank • Nazaré, Rio Negro, AM • 16/07/1999

Nest within a termite nest in a hollow tree • Habitat: Sub-montane forest, Lago Água Fria, PA • 13-15/02/1979



Partamona gregaria Pedro & Camargo, 2003



GENÉTICA
F.M.R.PRETO

118c(♂T-4)

São Luis do Tapajós
PA. Brasil
SB-21, 56°14'W; 4°26'S
14, 17-I-1979. Camargo

HOLOTYPE

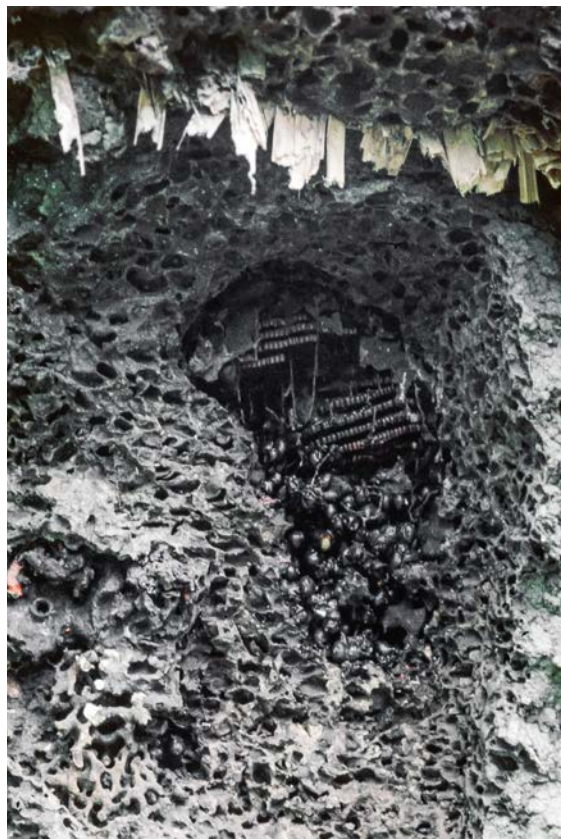
HOLOTYPE
Partamona gregaria Pedro & Camargo, 1988

Nest within an active termite nest in a building wall • Habitat: Sub-montane mixed forest, plateau and low plateaus, *campinas* (open fields on white-sand savannas). São Luís do Tapajós, PA • 14-17/01/1979

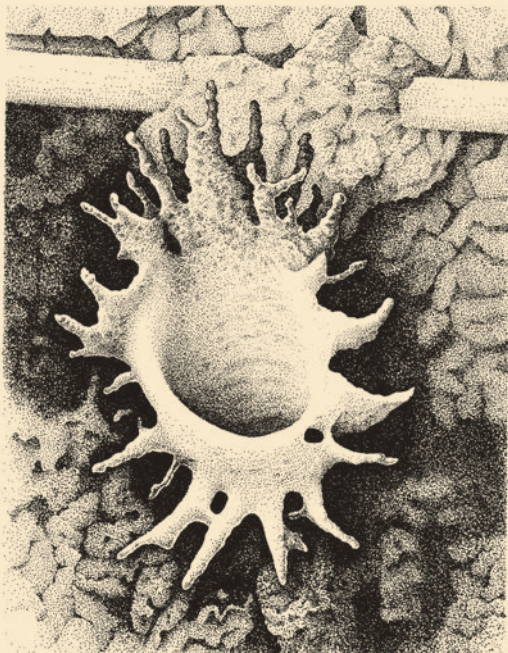


Nest in an active arboreal termite nest • Habitat: Terrace forests, Brazil nut stand • Mussum, 15 km S Aveiro, PA • 24-28/01/1979

Nest within an active termite nest in a building wall • Habitat: Dense floodplain forest and flattened relief • Tauari, PA • 29/01/1999



Partamona gregaria



Nest within an active termite nest in a building wall • Habitat: Mixed sub-montane forest, plateau and low plateaus, *campinas* • São Luís do Tapajós, PA • 14-17/01/1979

Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.



Partamona mourei Camargo, 1980



Carvoeiro
Rio Negro-
Rio Branco
Amazonas
16.VIII.24

Trigona (Partamona)
testacea var.
carvoeiroensis
H. F. Schwarz

PARATYPE

Partamona mourei
Camargo, 1980
Det. S. Pedro, 199

Partamona mourei

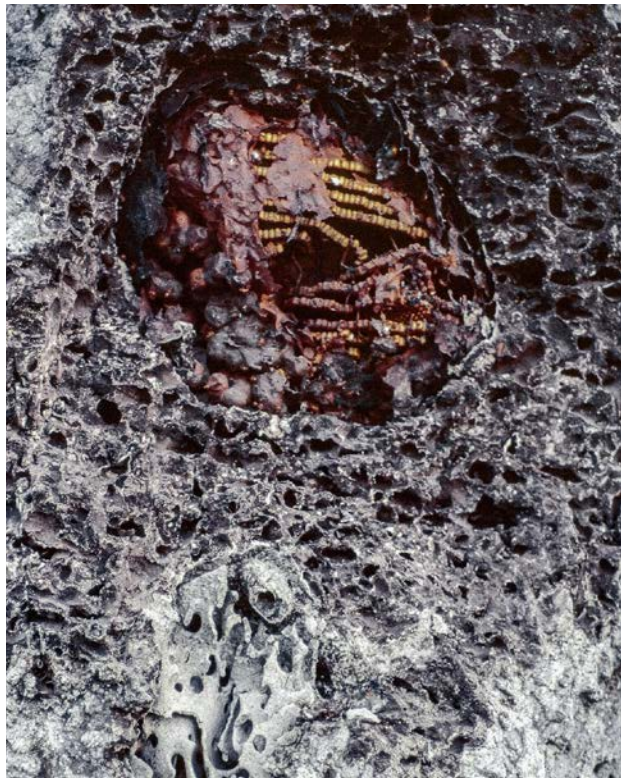


Nest within an arboreal termite nest • Habitat: Dense forest, plateau • Rio Carimum, PA • 16-17/02/1979

Nest within an active termite nest in a building wall • Habitat: Dense forest, lowlands, plateaus • Livramento, Rio Negro, AM • 24-26/07/1980



Nest within an active termite nest • Habitat: Sedimentary tablelands, transitional area, dissected relief • Caracaraí, RR • 13-15/08/1980



Nest within an active termite nest in a maripa palm trunk • Habitat: *Rocado* • Nazaré, Rio Negro, AM • 15/07/1999

Partamona nhambiquara Pedro & Camargo, 2003



Brasil, Rondônia
Guajará - Mirim
Sa. Pacaás Novos

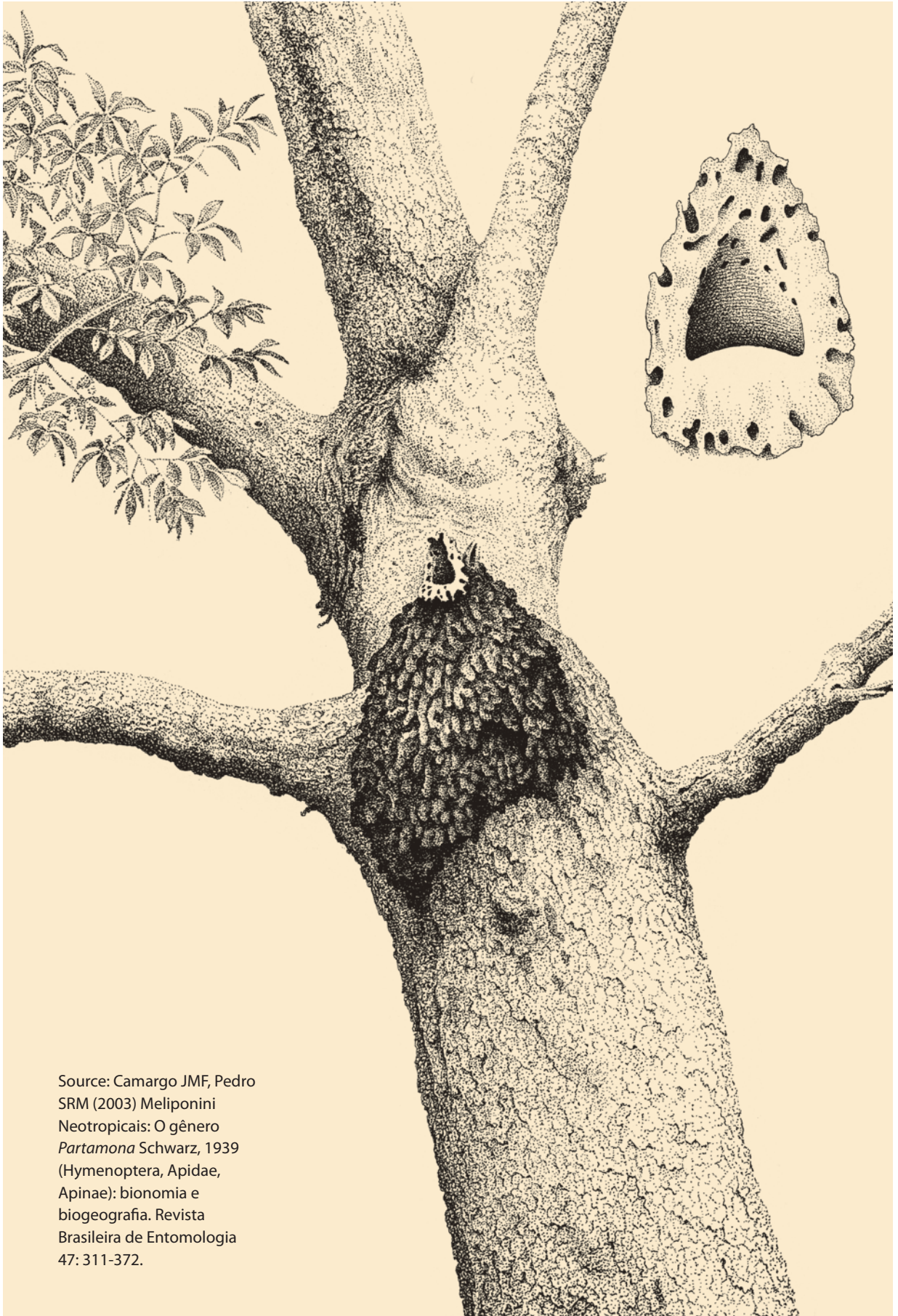
HOLOTYPE

28 / Janeiro / 1996
M.L. OLIVEIRA col.

HOLOTYPE
*Partamona
nhambiquara* Pedro
& Camargo, 1988

PN 0810

Partamona nhambiquara



Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.

Partamona pearsoni (Schwarz, 1938)



Kartabo
British Guiana
27.VI.1924

Trigona testacea
pearsoni ♀.
H.F. Schwarz

PARATYPE

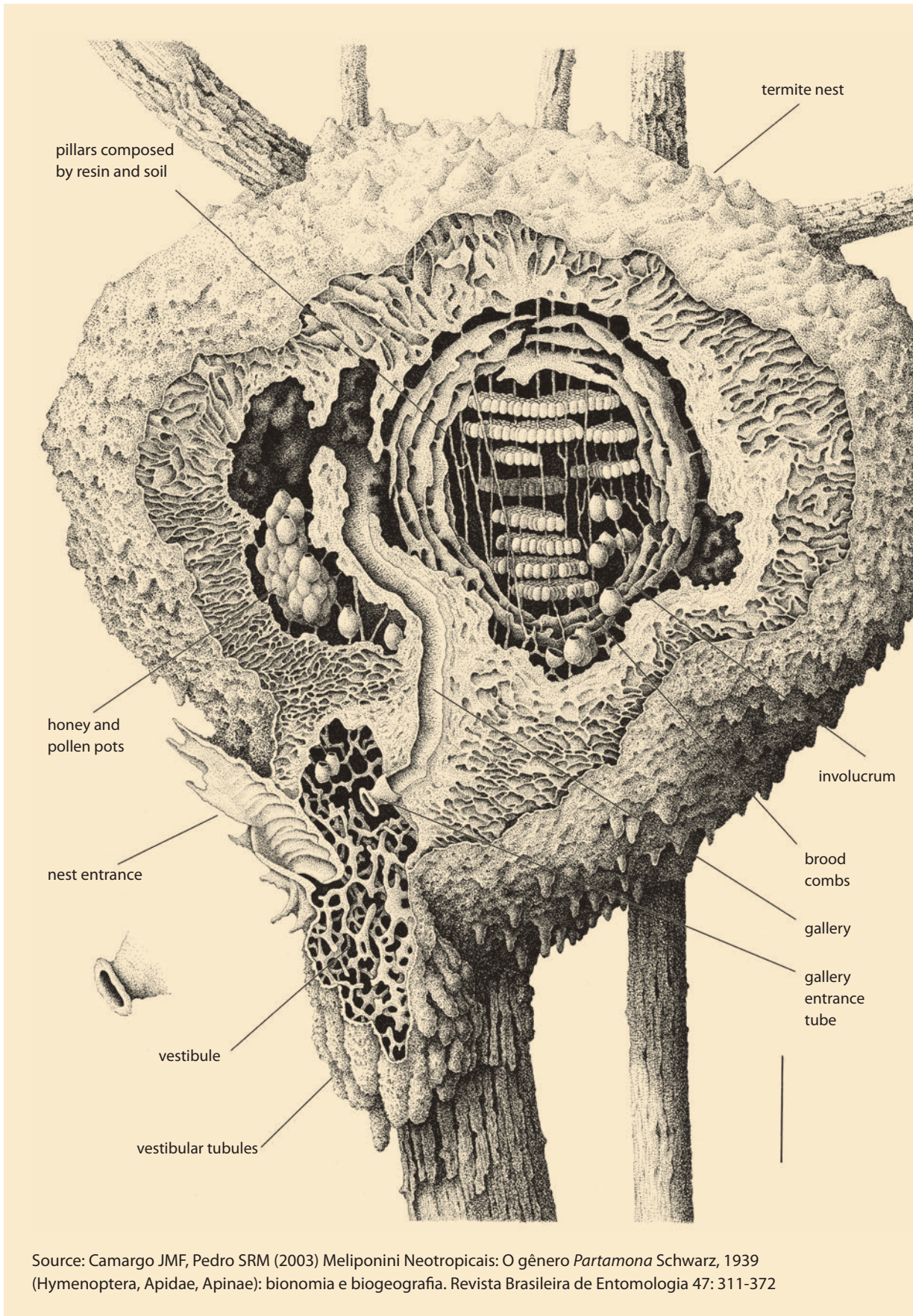
Collected by
Jay F. W. Pearson

Partamona pearsoni

Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.



Nest within an active arboreal termite nest • Habitat: Dense forest, lowlands, plateaus • Mouth of the Rio Marié, AM • 26-27/07/1980



Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372

Partamona testacea (Klug, 1807)

Visits açai (*Euterpe oleracea*) flowers.



Col. Perené PERU
26 June 1980

Cornell U.
Lot 589
Sub 375

PARATYPE

Trizona
(*Partamona*)
testacea var.
atahualpa
H. F. Schwarz

Partamona testacea
(Klug, 1807)
Det. S. Pedro, 1999



Underground nest close to tree trunk • Habitat: Terra firme forest next to *Igapó* forest • Vendaval, Rio Solimões, AM • 17/01/1977

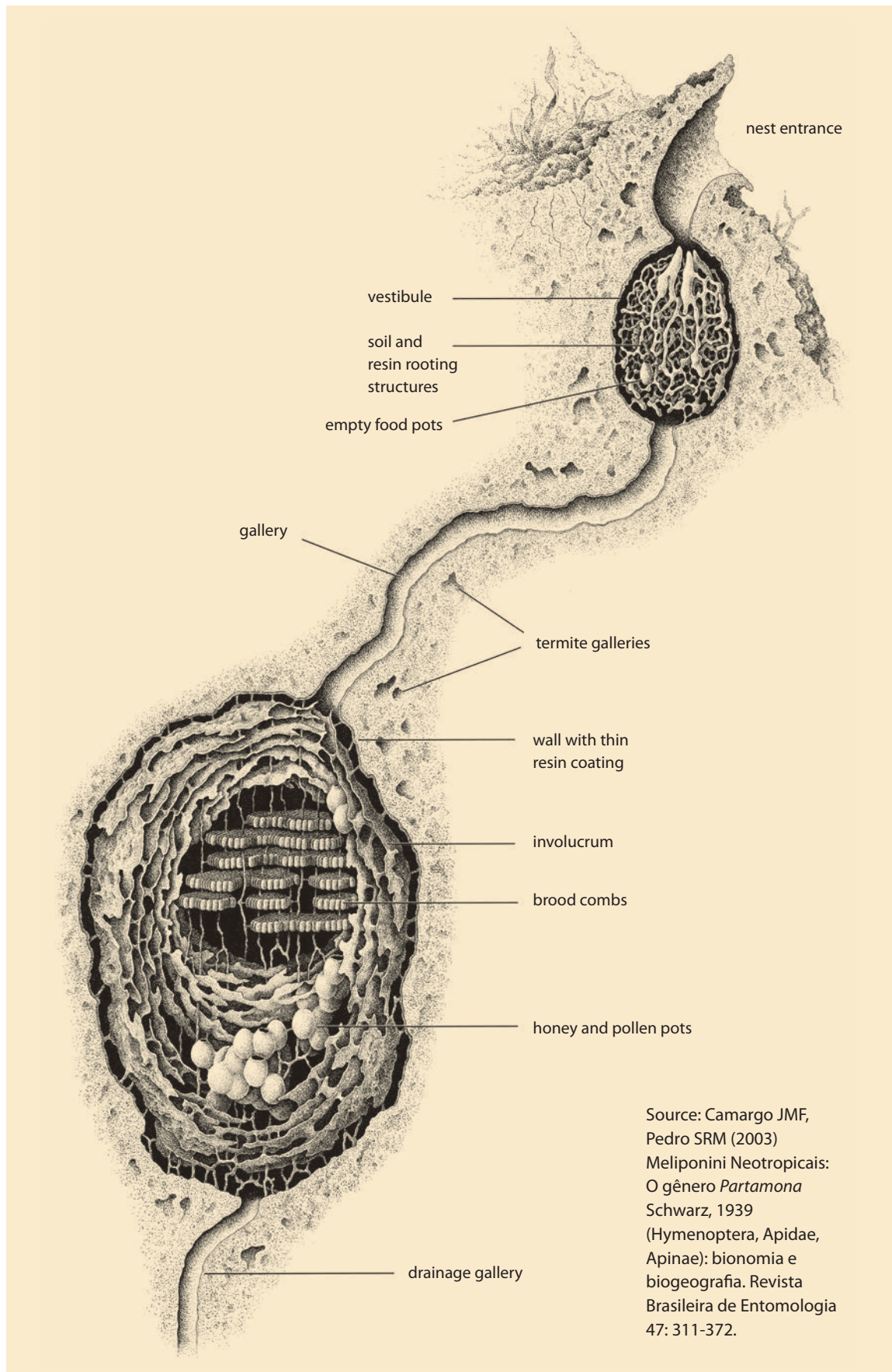


Underground nest close to tree trunk (termites are present) • Habitat: Terra firme forest next to *Igapó* forest • Vendaval, Rio Solimões, AM • 16/01/1977

Partamona testacea

Underground nest • Habitat:
Terra firme field; forest felled in
1990 • Bacururu, Rio Juruá, AM
• 30/07/1993





Source: Camargo JMF,
Pedro SRM (2003)
Meliponini Neotropicais:
O gênero *Partamona*
Schwarz, 1939
(Hymenoptera, Apidae,
Apinae): bionomia e
biogeografia. Revista
Brasileira de Entomologia
47: 311-372.

Partamona vicina Camargo, 1980

Common name:
kangàrrà-kàk-ti.

Visits Brazil nut
(*Bertholletia excelsa*)
flowers.



Z-21c, ♀

Barra do Garças
MT., BRASIL
10.24. I. 1977
Col. Camargo

HOLOTYPE ♀
P. (Partamona)
vicina
Camargo, 1977

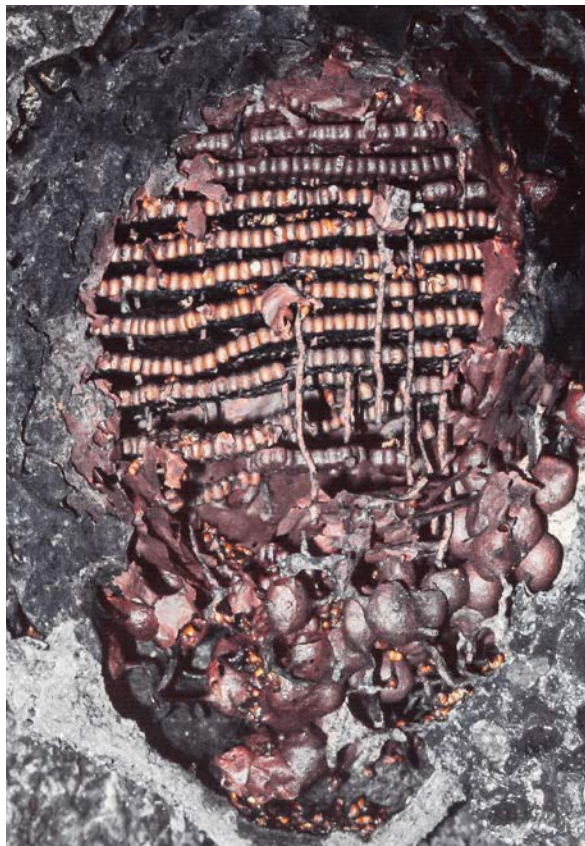




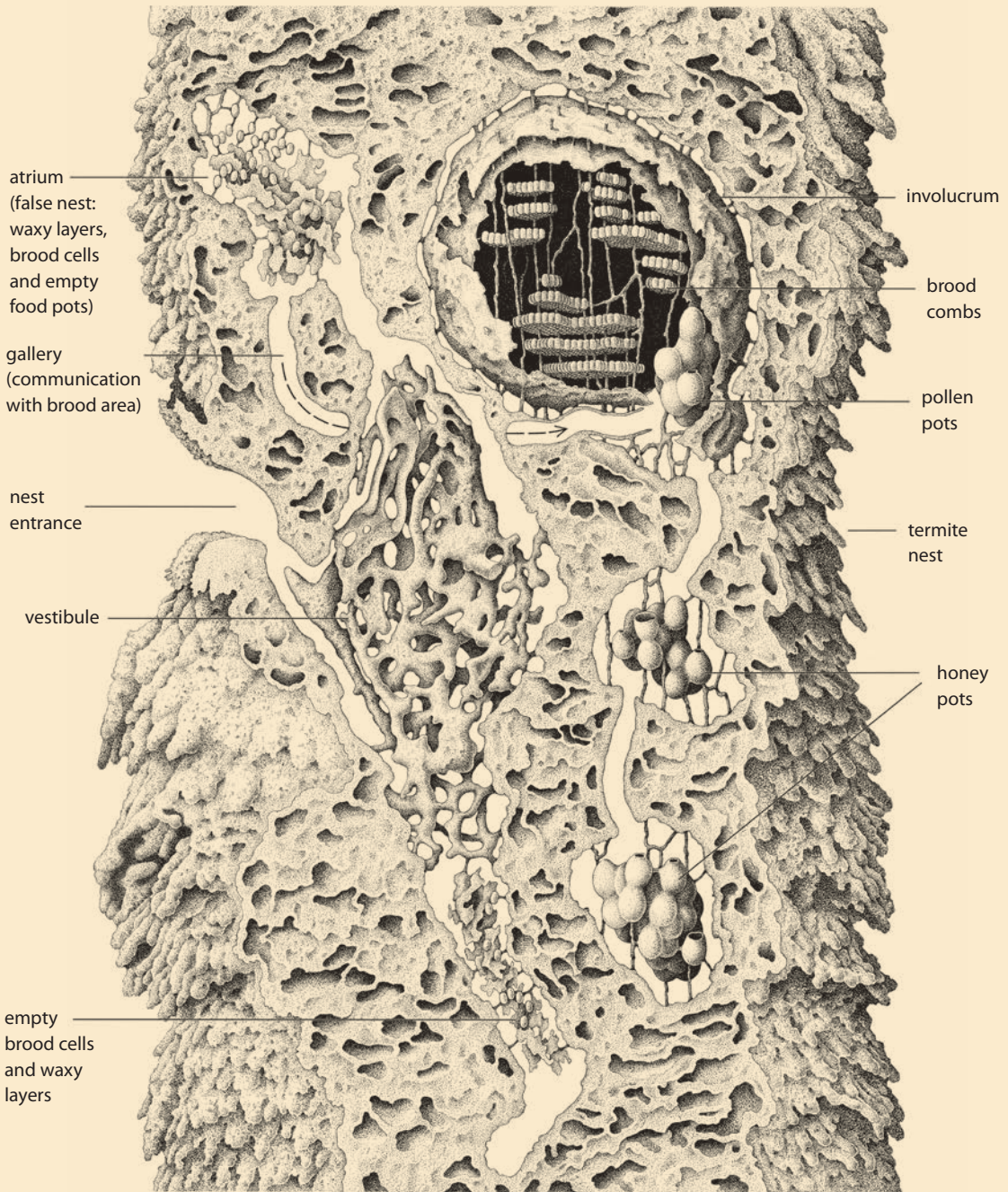
Nest within an active termite nest in a building wall • Habitat: Cerrado enclave • Alter do Chão, PA • 03-04/02/1979



Nest within an active termite nest in a building wall • Habitat: Dense floodplain forest and flattened relief • Tauri, PA • 01-29/01/1979



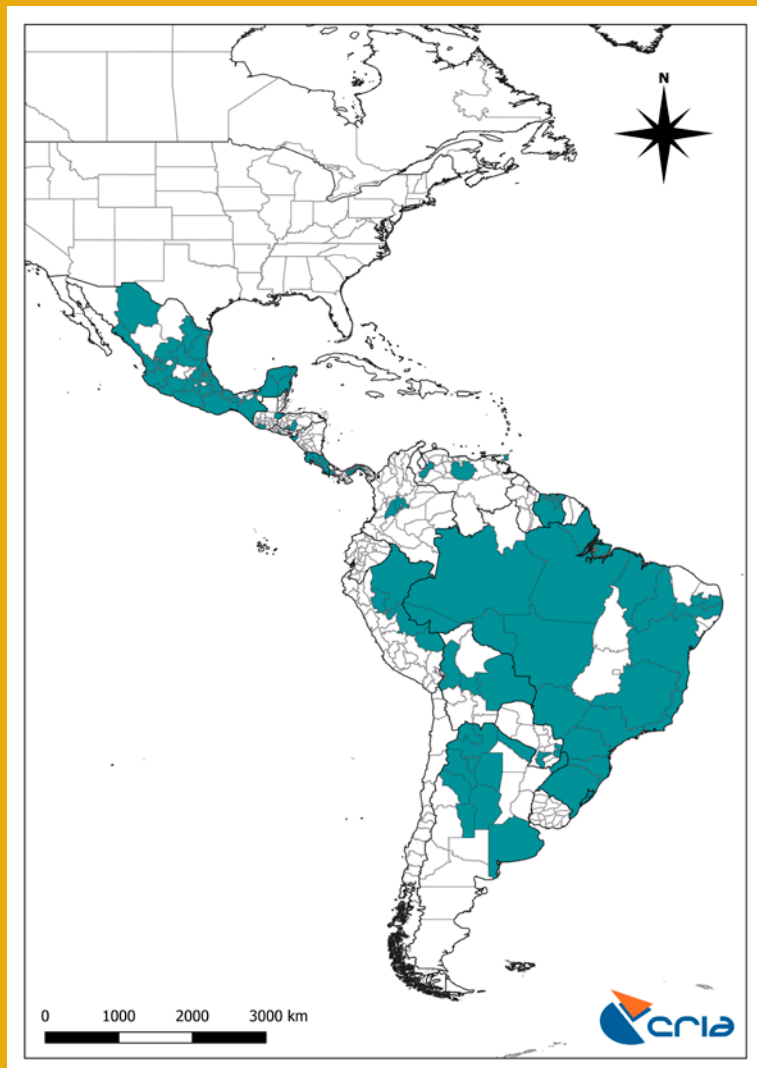
Nest within arboreal termite nest • Habitat: Terrace forest, Brazil nut stand • Mussum, 15 km S Aveiro, PA • 24-28/01/1979



Source: Camargo JMF, Pedro SRM (2003) Meliponini Neotropicais: O gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae): bionomia e biogeografia. Revista Brasileira de Entomologia 47: 311-372.

Genus

Plebeia Schwarz, 1938



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lepageletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Plebeia alvarengai Moure, 1994

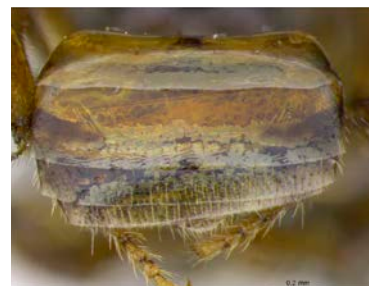


Rio Trairão. PA – Brasil
(50 km NE Gradaús)

SB-22,51°49'W,7°21'S
21,24-VII-79. Mazucato

Plebeia minima (Gribodo, 1893)

Common name: lameojos.
Visits açai (*Euterpe oleracea*)
flowers.



Barra do Garças
MT. BRASIL

21. I. 1971
Col. Camargo

P. (Plebeia)
minima
(Gribodo, 1893)
Det. Camargo 1979

Plebeia minima



Nest entrance in a fence post cavity • Habitat: Dense forest, lowlands • Livramento, Rio Negro, AM • 24-26/07/1980



Nest within a dry *capitari* branch • Habitat: *Igapó* beach, margin of the Lago Tefé • Nogueiras, Lago Tefé, AM • 25/08/1993



Nest within a fence post cavity • Habitat: Dense forest, lowlands • Livramento, Rio Negro, AM • 24-26/07/1980

Plebeia variicolor (Ducke, 1916)



RIO IPIXUNA
Purus-AM-Brosil
20,23-I-1986

58.20,63°20'W-6°0'S
Camargo - Mazucato

*Plebeia
variicolor*
(Ducke, 1916)
Det. Moure 1987

Genus

Ptilotrigona Moure, 1951

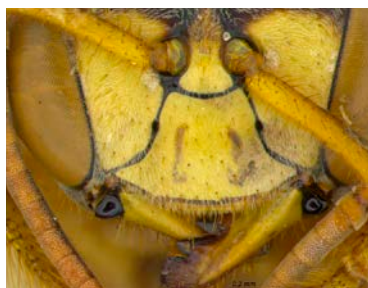


Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Camargo JMF, Pedro SRM (2004) Meliponini neotropicais: o gênero *Ptilotrigona* Moure (Hymenoptera, Apidae, Apinae). Revista Brasileira de Entomologia 48: 353-377.

Ptilotrigona lurida (Smith, 1854)

Common names: aramá,
borá-boi, borá-cavalo, borá,
tataíra-grande, abelha-
piranha, moça-branca.



Sao Paulo de Olivença
AM, Brasil. SA-19.69-4b

19,20-I-1977, Camargo
M. Mazucato leg.

T. (Ptilotrigona)
lurida *lurida*
Smith, 1854
Det. Camargo 1977





Nest within a hollow tree • Habitat: Sub-montane forest • Location: Mouth of the Rio Curicuriari, AM • Data: 15-21/07/1980



Nest within a live tree cavity • Habitat: *Terra firme* forest, caatinga type • Tapurucuara Mirim, Rio Negro, AM • 04/07/1999



Nest entrance in a hollow tree • Habitat: Cerrado enclave • Alter do Chão, PA • 03-04/02/1979

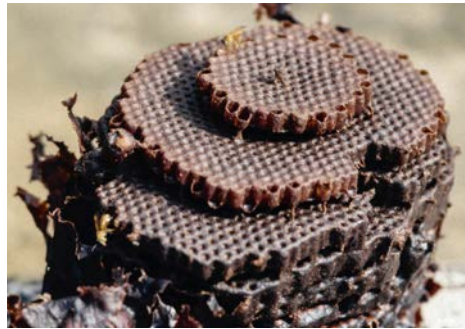


Nest entrance in a live *macaricão* tree cavity • Habitat: *Terra firme* forest • Camanaus, Rio Negro, AM • 29/06/1999

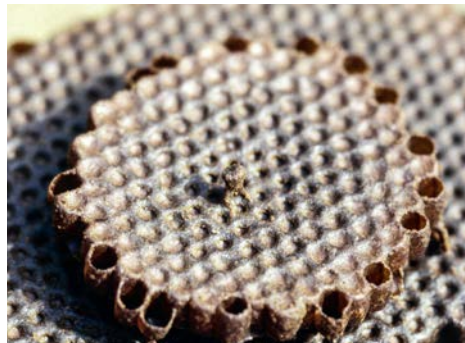
Ptilotrigona lurida



Nest within a hollow tree • Habitat: Sedimentary tablelands, transitional area, dissected relief • Caracará, RR • 13-15/08/1980



Brood combs • Habitat: Sub-montane forest, dissected relief • Mouth of the Rio Curicuriari, AM • 15-21/07/1980



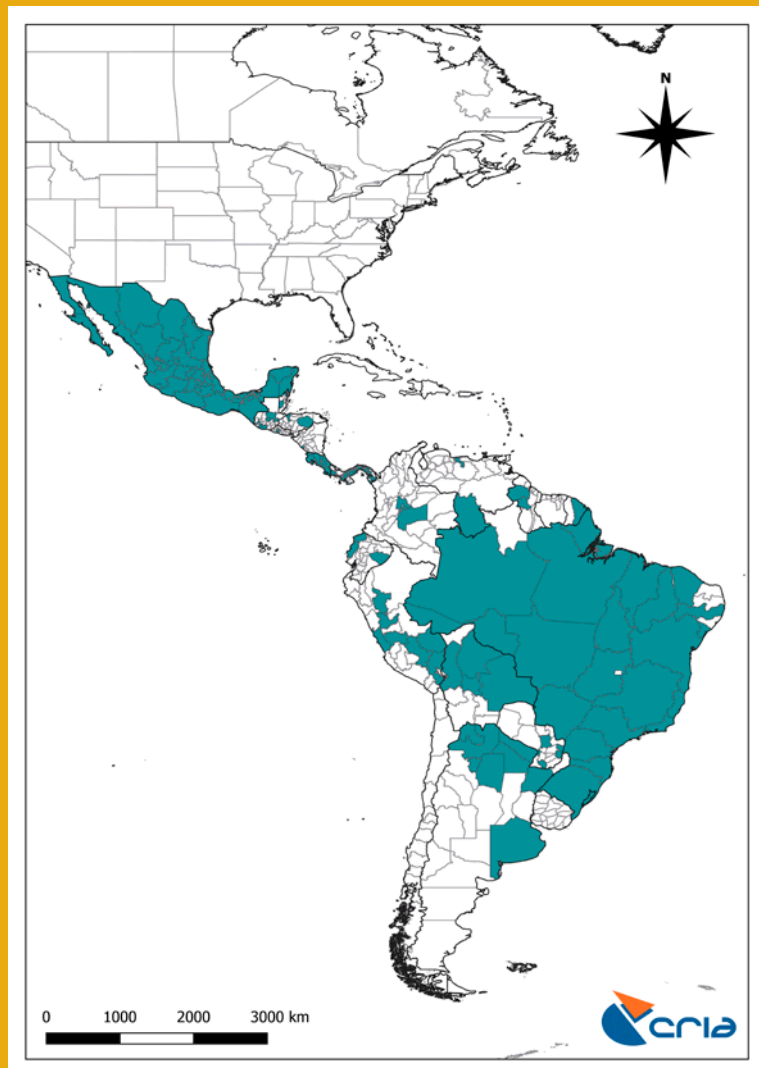
Larvae in a comb • Habitat: Cerrado enclave • Alter do Chão, PA • 03-04/02/1979



Pots contain *Candida* yeast that causes dehydration of the stored pollen • Habitat: Sub-montane forest, dissected relief • Mouth of the Rio Curicuriari, AM • 15-21/07/1980

Genus

Scaptotrigona Moure, 1942



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Scaptotrigona bipunctata (Lepeletier, 1836)

Common names:

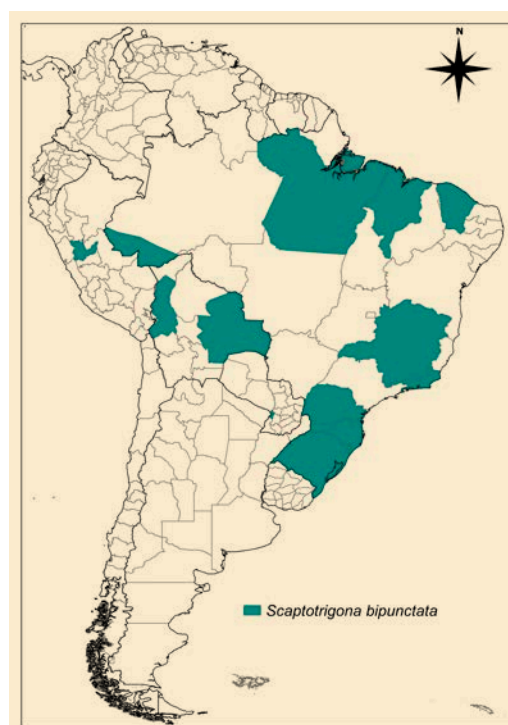
canudo, tubuna, tapesuá.

Pollinates carrot (*Daucus carota*), sunflower (*Helianthus annuus*) and canola (*Brassica napus*) flowers. Visits coffee (*Coffea arabica*) flowers.



BRAZIL
Paraná
Curitiba
1 Nov. 1942

*Scaptotrigona
bipunctata*
Lepeletier, 1836
Det. Camargo, 1996



Scaptotrigona polysticta Moure, 1950

Common names:
benjoi, bijui,
abelha-canudão,
mijui, bui-kaiaki,
imrê-ti.



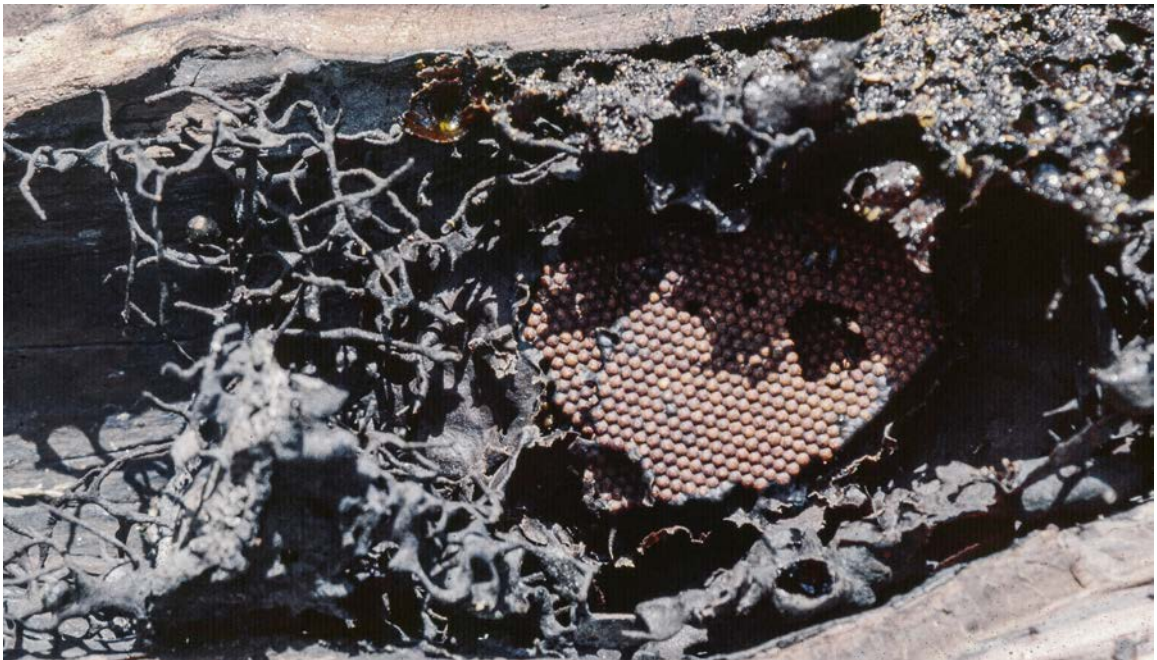
Conceição das Alagoas
SE-22,48-20a MG Brasil
20-IX-1973 Pêna leg.

Scaptotrigona polysticta

Nest entrance in a hollow tree
• Habitat: Sub-montane forest,
dissected relief • Cachoeira da
Porteira, PA • 09-12/02/1979



Nest entrance in an *acapú* tree
cavity • Habitat: Tall *terra firme*
forest, Brazil nut stand • Maraã,
Rio Japurá, AM • 16/08/1993



Nest within a hollow tree •
Habitat: Sub-montane forest,
dissected relief • Cachoeira da
Porteira, PA • 09-12/02/1979

Scaptotrigona postica (Latreille, 1807)

Common names:
mandaguari, canudo,
timba-amarela.

Pollinates umbu (*Spondias tuberosa*) flowers and visits coffee (*Coffea arabica*), murici (*Byrsonima crassifolia*) and yellow mombin (*Spondias mombin*) flowers.



Aragarcas
GO., BRASIL
10.24.I. 1971
Col. Camargo

Scaptotrigona postica



Nest within a live *cooti* tree cavity • Habitat: Gallery forest, *brejo* (marsh), surrounded by cerrado • Krahó Reserve, Galheiros, TO • 20/01/1993



Nest within a live *pau-terra* tree cavity • Habitat: Typical cerrado • Mateiros, TO • 10-12/07/1995



Nest within a live *coóti* tree cavity • Habitat: Gallery forest, *brejo*, surrounded by cerrado • Krahó Reserve, Galheiros, TO • 20/01/1993

Genus

Scaura Schwarz, 1938

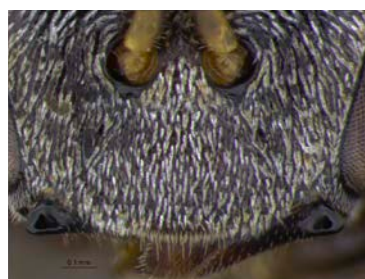


Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Nogueira DS, Santos-Júnior JE, Oliveira FF, Oliveira ML (2019) Review of *Scaura* Schwarz, 1938 (Hymenoptera: Apidae: Meliponini). Zootaxa 4712:451-496.

Scaura latitarsis (Friese, 1900)

Common names:
pegoncito,
sharabata,
txashkù-mexupa.



RIBEIRÃO PRETO
S. Paulo - BRASIL

3-VIII-1979
Col. Zucchi

S. (Scaura)
latitarsis (Friese)
Det. Camargo 1979



Nest entrance

Nest within a live arboreal termite nest
• Habitat: Dense forest,
lowlands, plateaus • Aruti, Rio
Negro, AM • 22-23/07/1980



Brood combs within a live termite nest found in a tree branch •
Habitat: *igapó* forest • Santa Isabel do Rio Negro, AM • 11/07/1999

Scaura latitarsis

Brood combs within an arboreal termite nest • Habitat: Dense forest, lowlands, plateaus • Aruti, Rio Negro, AM • 22-23/07/1980



Food pots within a live arboreal termite nest • Habitat: Dense forest, lowlands, plateaus • Location: Aruti, Rio Negro, AM • 22-23/07/1980

Scaura longula (Lepeletier, 1836)

Common names:
jataí-negra, jataí-
preta, ramichi-negra-
grande, mehnô-rã-tyk.



LUZIANIA
JATIARA
GO. BERAEL
19.1.1991
UNIVERSITA. NISTO

*Scaura
longula*
(Lep. 1836)
Det. Carrasco, 1991

Scaura longula



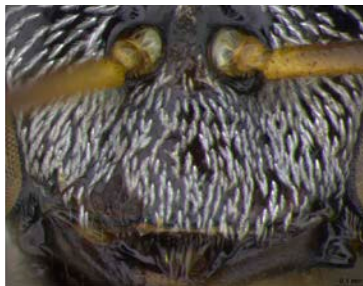
Nest entrance in a live tree cavity • Habitat: *Igapó* • Ponta do Gavião, Rio Negro, AM • 31/07/1999



Vertical brood combs • Habitat: *Igapó* • Ponta do Gavião, Rio Negro, AM • 31/07/1999

Scaura tenuis (Ducke, 1916)

Common name:
ramichi-negra.



FONTE BOA. AM. Brasil
SA-19,66-3f,xii

24,25-I-1977, Camargo
M. Mazucato leg.

S. (Scaura)
tenuis (Ducke.)
Det. Camargo 1977

Scaura tenuis



Nest entrance • Habitat: Broadleaved, open forest and floodplain • Santa Maria, Itaituba, PA • 18-20/01/1979



Nest within a rotten trunk
• Habitat: *Igapó* • Ponta do Gavião, Rio Negro, AM • 31/07/1999



Nest within a termite nest
• Habitat: *Várzea* forest • Igapó Jaraqui, Rio Juruá, AM • 28/07/1993

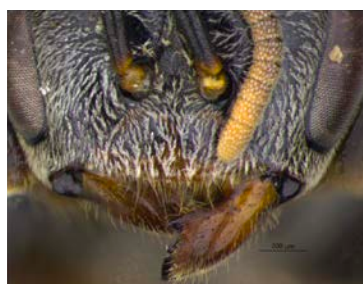
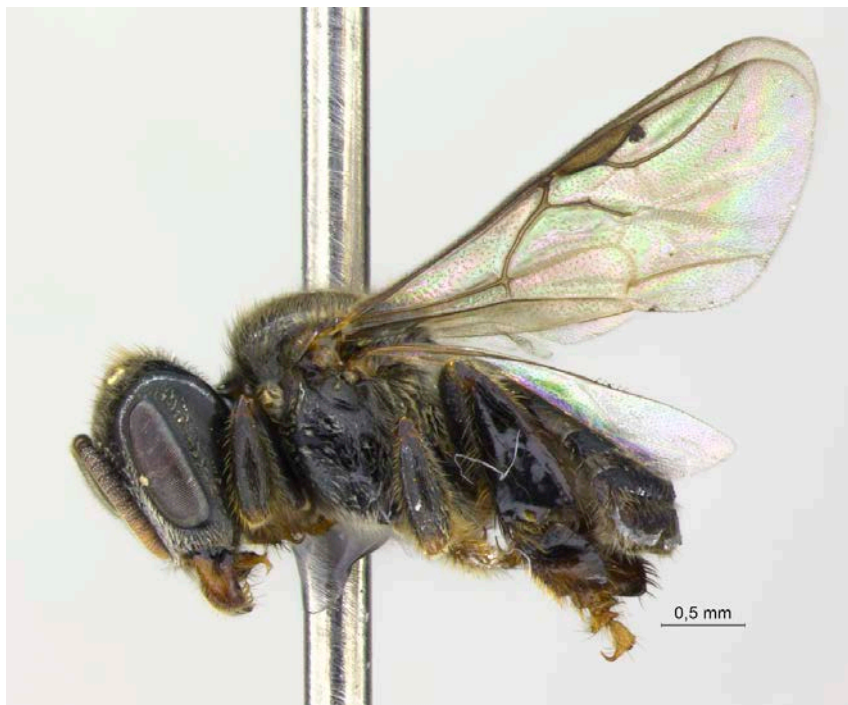
Genus

Schwarzula Moure, 1946



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Schwarzula coccidophila Camargo & Pedro, 2002



RPSP
878c

Tapuruçara-mirim,
rio Negro, AM, BRASIL
00°23'28"S, 66°26'07"W
15.II.2001 Camargo leg.



HOLOTYPE
Schwarzula
coccidophila
Camargo & Pedro
2002



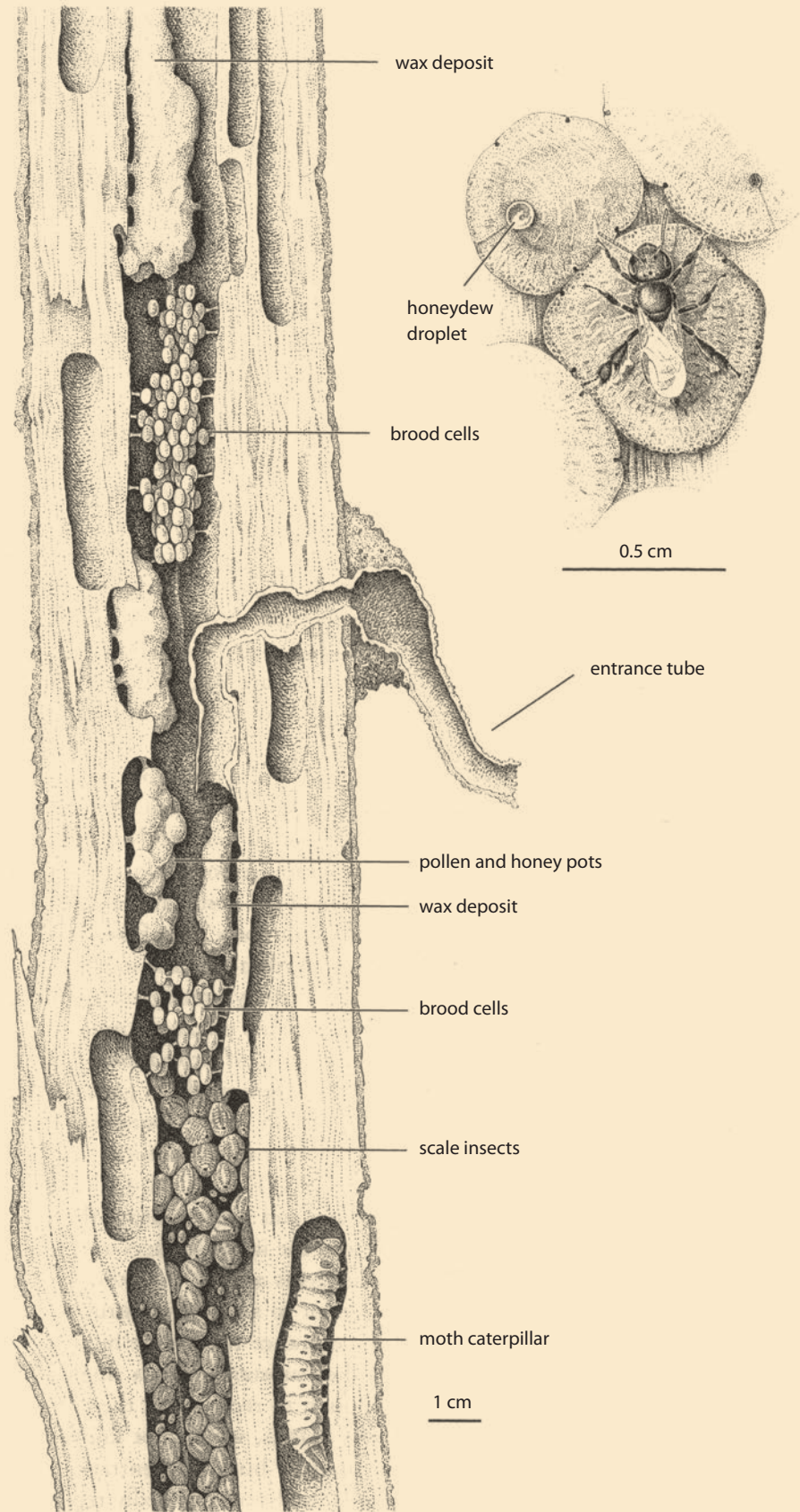
Nest entrances

Scale insects within
S. coccidophila nest

Nests within galleries excavated
by moth larvae (*Cossula* sp.), in
cumandá branches • Habitat:
igapó forest, riverbank •
Tapurucuara Mirim, Rio Negro,
AM • 02/15/2001



Schwarzula coccidophila



Source: Camargo JMF, Pedro SRM (2002) Mutualistic association between a tiny Amazonian stingless bee and a wax-producing scale insect. *Biotropica* 34: 446-451.

Schwarzula timida (Silvestri, 1902)

Common names:
lambe-olhos, frecheira,
mosquito-do-ouvido.



PARALECTOTYPE
Schwarzula timida
(Silvestri, 1902)
Des. Camargo, 1984

11 COXIPÓIS
da coleção Silvestri
de Portici

Genus
Tetragona Lepelletier &
Serville, 1828



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lepelletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Tetragona clavipes (Fabricius, 1804)

Common names: borá, vorá, vamos-embora, i-kàikà.

Pollinates cassava (*Manihot esculenta*) flowers and visits coffee (*Coffea arabica*), guava (*Psidium guajava*), acerola (*Malpighia punicifolia*) and cotton (*Gossypium hirsutum*).

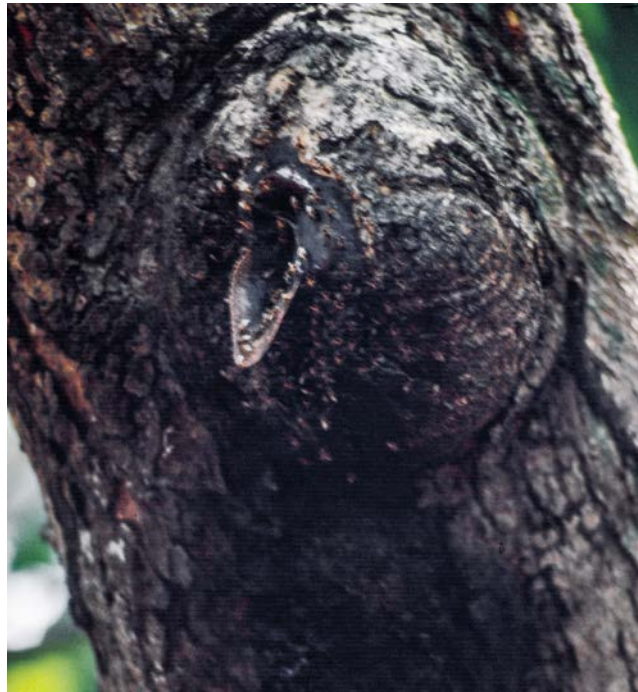


FRENCH GUIANA: Sinnamary
10 km SE; palm planta-
tion rd. 2 May 1982
D. Roubik coll. No. 63

(Tetragona)
clavipes Fab.
det. D. Roubik '82



Nest entrance within
a mango tree cavity •
Habitat: Cerrado mixed
with gallery forest •
Lizarda, 60 km L, MA •
11/18/1994



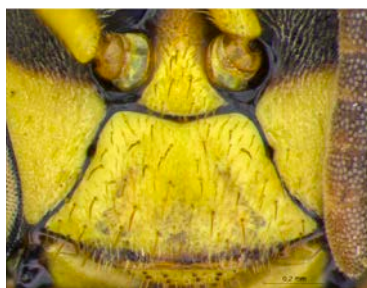
Brood combs removed
from a live *taubarana*
tree cavity, at more
than 20 m above the
ground • Habitat:
Igapó forest • Forte da
Graça, Rio Juruá, AM •
04/08/1993



Nest within dead tree
cavity • Habitat: *Terra
firme* forest, next to the
roçado • Lago Uará,
Rio Solimões, AM •
10/08/1993

Tetragona dorsalis (Smith, 1854)

Common names:
borá-bico-de-vidro,
tôtn-my, tôtn-my're.



SAO LUIS- MA.
Brasil: 24-XII
• 1982
822540

MaZuçato, Aily
Camargo leg.



Nest entrance



Nest within a live *coóti* tree cavity • Habitat: Gallery forest, *brejo*, surrounded by cerrado • Krahó Reserve, Galheiros, TO • 20/01/19



Tetragona goettei (Friese, 1900)

Common names:
tataíra-pequena,
mehr-si-we'i,
shawa-puiki-buná.

Visits Brazil nut
(*Bertholletia excelsa*)
flowers.



Sao Paulo de Olivença
AM, Brasil, SA-19,69-4b

19,20-I-1977, Camargo
M. Mazucato leg.

T. (Tetragona)
goettei Fr., 1900
Det. Camargo 1979





Nest entrance in a rotten, dead tree cavity • Habitat: *Terra firme* forest, next to *igapó* forest (Rio Jacaré) • Arimã, Purus, AM • 07/02/1986



Brood combs from nest within a hollow tree • Habitat: Terrace forest, Brazil nut stand • Mussum, 15 km S Aveiro, PA • 24-28/01/1979

Tetragona handlirschii (Friese, 1900)



Ilha de Maracá - RR
Brasil 5-10/10/1987
Lucio A.O. Campos
Marcos V. B. Garcia

*Tetragona
handlirschii*
(Friese, 1900)
Det. Camargo 1987

Tetragona kaieteurensis (Schwarz, 1938)

Visits Brazil
nut (*Bertholletia
excelsa*) flowers.



COLEÇÃO
CAMPOS SEABRA

J. Braga 1100

OBIDOS
Pará - BRASIL
IX-1954

EPD

prov. syn. de
kaieteurensis
Schwarz

*Tetragona
melanospila*
Moure, 1963
Det. MOURE 1963

*Tetragona
taigonospila*
Moure, 1999
Det. Camargo, 2008

= *kaieteurensis*
Schwarz, 1938
Det. Camargo, 2008

Tetragona quadrangula (Lepelletier, 1836)

Common name:
menire-udja.



S. PARAIPO-MG
Brasil-VI-61
G. Elias leg.

(*Tetragona*)
clavipes
Det. Moure. 1966





Nest entrance



Nest within a live *ubeiro* tree cavity •
Habitat: *Brejo* forest, together with buriti
palm stand, surrounded by cerrado •
Krahó Reserve, Galheiros, TO • 19/01/1993

Tetragona truncata Moure, 1971

Common names:
borá-de-canudo, õ-i.



Aragarças
G.O. - BRASIL

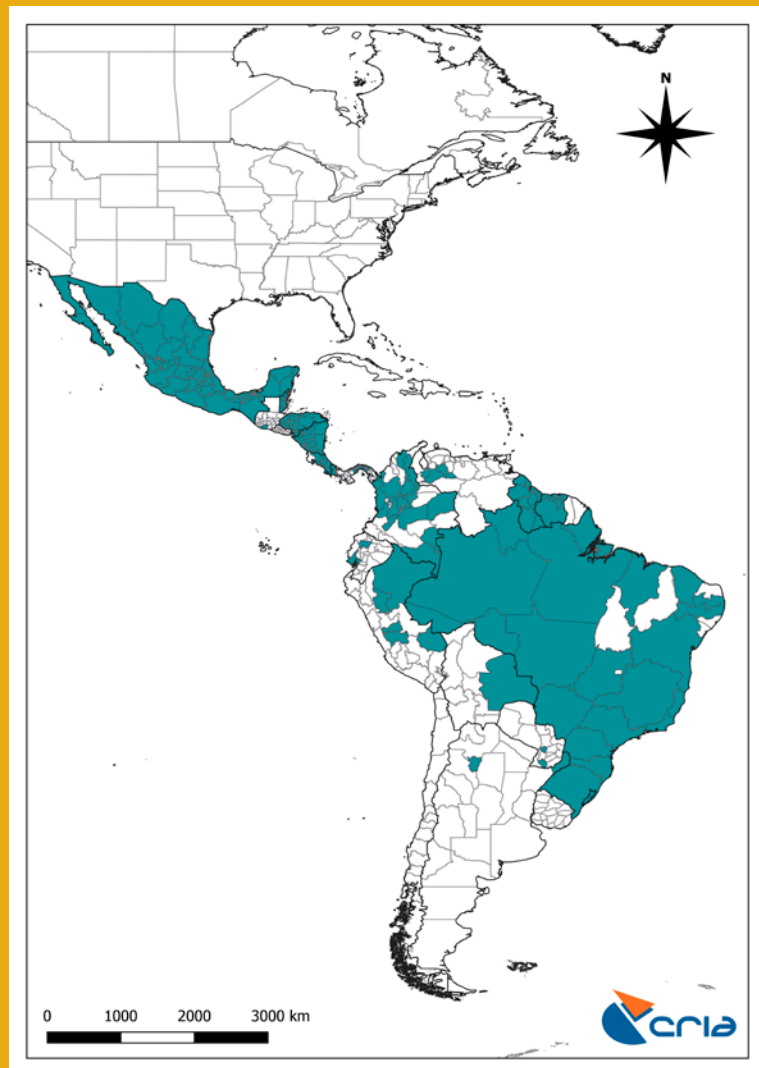
10.24.I. 19 71
Col. W.E. Kerr

PARATYPE

T.(*Tetragona*)
truncata
Moure, 1971

Genus

Tetragonisca Moure, 1946



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lepageletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Tetragonisca angustula (Latreille, 1811)

Common names: jataí, jataí-verdadeira, vangelitas, maria-seca, virginitas, virgencitas, abelhas-ouro, mosquitinha-verdadeira, my-krwàt.

Pollinates strawberry (*Fragaria x ananassa*), avocado (*Persea americana*), umbu (*Spondias tuberosa*), annato (*Bixa orellana*), bell pepper (*Capsicum annuum*), orange (*Citrus sinensis*), mandarin orange (*Citrus reticulata*), mango (*Mangifera indica*), canola (*Brassica napus*), onion (*Allium cepa*), acapu (*Vouacapoua americana*), cupuaçu (*Theobroma grandiflorum*), wild carrot (*Daucus carota*), cucumber (*Cucumis sativus*), coffee (*Coffea arabica*), watermelon (*Citrullus lanatus*) and acerola (*Malpighia punicifolia*) flowers.



RITAPOLIS-MG, BRASIL
SF-23,44-21d/19-I-1974

M.Mazucato, Vellhuis
J.M.F.Camargo leg.





Nest entrance in a dry tree cavity • Habitat: *Roçado, terra firme* • Nogueiras, Lago Tefé, AM • 26/08/1993

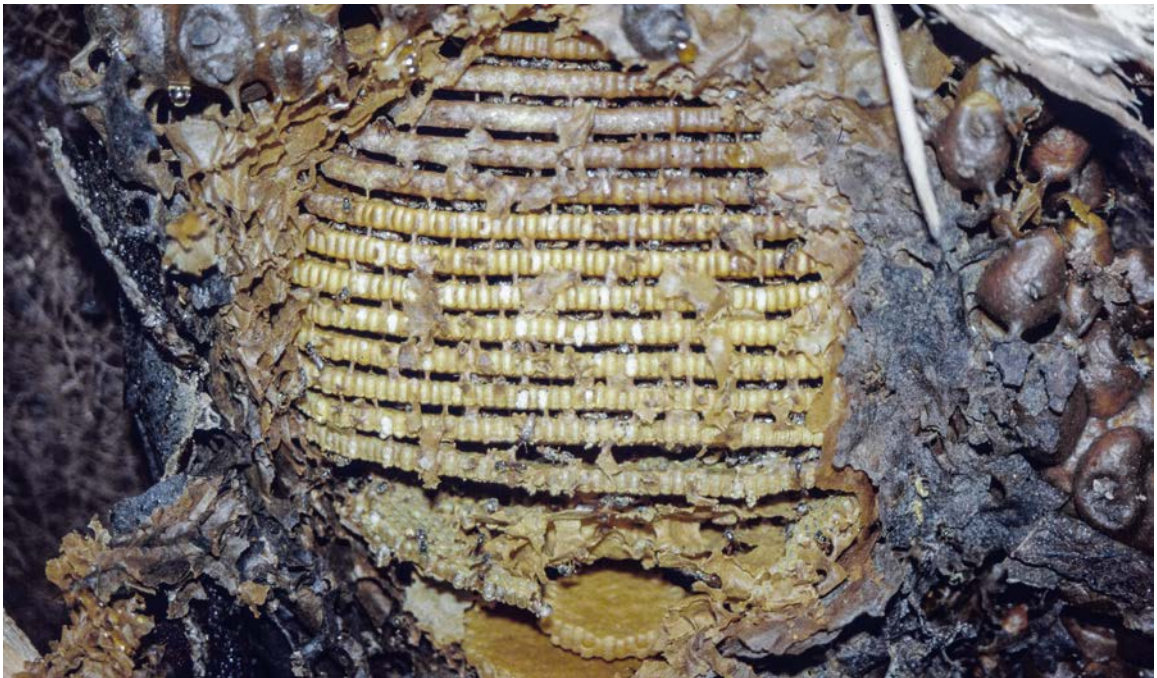


Nest entrance in a hollow at the base of an enormous *tauari* trunk • Habitat: *Terra firme* forest • Maraã, Rio Japurá, AM • 17/08/1993



Nest within a dead tree cavity • Habitat: Dense forest, lowlands • Curiauí Lake, Rio Negro, AM • 24-25/08/1980

Tetragonisca angustula



Nest within a hollow at the base
of an enormous *tauari* trunk •
Habitat: *Terra firme* forest • Maraã,
Rio Japurá, AM • 17/08/1993

Genus

Trigona Jurine, 1807



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Trigona albipennis Almeida, 1995



Nogueiras, lago de Tefé
AM-Brasil - 25-26.08.1993
64° 48' W, 3° 19' S

Camargo, Pedro,
Mazúcato, leg.

*Trigona
albipennis*
Almeida, 1995
Camargo, m
Det. Camargo, 1999





Nest within a live arboreal termite nest (in vine) • Habitat: Tall várzea forest • Camaruã, Purus, AM • 29/01/1986



Brood combs (top) and food pots (bottom)



Nest within a live termite nest, fixed to an embauba tree and vines
• Habitat: Várzea, island • Paraíso, Rio Japurá, AM • 20/08/1993

Trigona amazonensis (Ducke, 1916)

Common names: xupé-grande, xupé-mangangá, mangangá, amo, cortapelo, arapuá-preto-médio, txashku-buiki, nawa-bakû, ku-krâi-ti, abeja-arambaso. Visits Malay apple (*Syzygium malaccense*) flowers.



ECUADOR: PAST, 1000m
Llandia (17 km N. Puyo)
20 VII 1994, F. Génier
remnant rain for., feces tr.

Trigona amazonensis
(Ducke, 1916)
sensu Schwarz
Det. Camargo, 1996





Exposed nest in a jauari palm tree, at 10 m above the ground

• Habitat: Tall *terra firme* forest, Brazil nut stand • Camaruã, 15 km, Purus, AM • 31/01/1986



Nest fixed to a live tree trunk

• Habitat: *Várzea* • Paraíso, Rio Japurá, AM • 20/08/1993



Arboreal nest, fixed to a trunk

• Habitat: Dense forest, island • Camanaus, Rio Negro, AM • 12-14/07/1980

Trigona amazonensis

Nest entrance



Brood combs from an exposed nest fixed to a trunk • Habitat: Dense forest, island • Camanaus, Negro River, AM • 12-14/07/1980



Trigona branneri Cockerell, 1912

Common names: guaxupé, abelha-corta-cabelo, arapuá, irapuá, topoé-negra, mehñy-tyk, nawa-bakû, mbulo-oni, kankantii-oni.
Pollinates acapu (*Vouacapoua americana*) and camu-camu (*Myrciaria dubia*) flowers. Visits Brazil nut (*Bertholletia excelsa*) flowers.



L A G O A G U A F R I A , P A .
Rio Trombetas - BRASIL

SA.21.X-C,56°51'W,1°25'S
13-15.II-1979. Camarao

T. (Trigona)
branneri CKH, 1912
Det. Camarao 19 79

Trigona branneri



Exposed nest fixed to a *tucumã* trunk, at 3 m above the ground • Habitat: *Roçado, terra firme* • Bacururu, Juruá River, AM • 01/08/1993

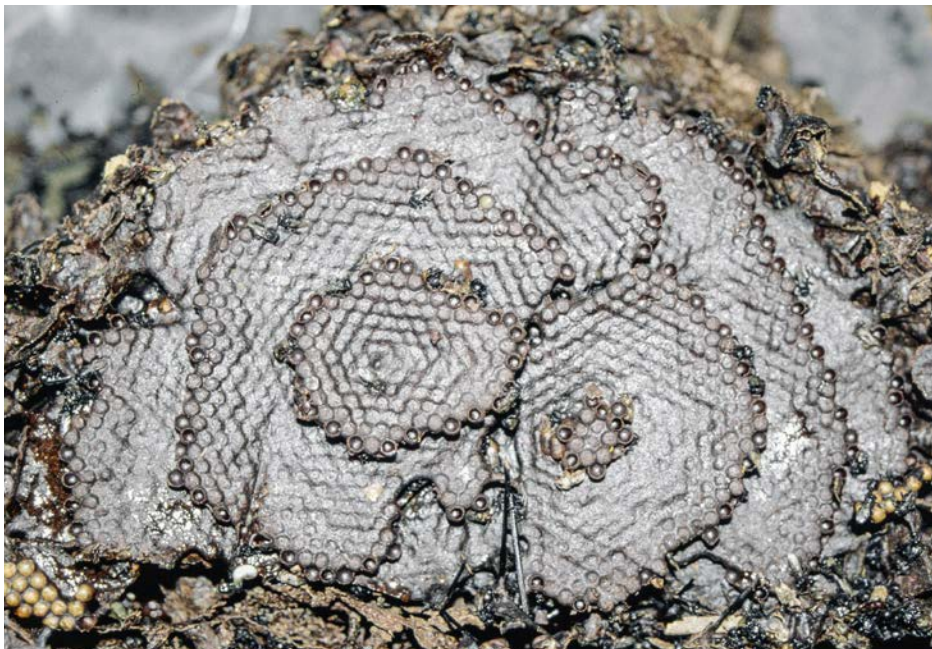


Arboreal nest fixed to a jauari palm trunk • Habitat: Terra firme, *igapó* margin, Tall forest of Brazil nut trees • Ipixuna, Purus 57 km, Tapauá, AM • 17/01/1986

Trigona branneri



Brood combs from an exposed nest fixed to a *tucumã* trunk, at 3 m above the ground • Habitat: *Roçado, terra firme* • Bacururu, Rio Juruá, AM • 01/08/1993



Trigona chanchamayoensis Schwarz, 1948

Common names:
cupira, imrê-ti-re,
arapuá-amarelo-menor.



Puyo, Oriente
Ecuad. 27. 5. 38

Coll.
F.M. Brown

PARATYPE

Trigona (Trigona)
chanchamayoensis
H. F. Schwarz





Nest within an arboreal termite nest, also inhabited by *taragua* ants • Habitat: Dense floodplain forest and flattened relief • Tauari, PA • 01-29/01/1979



Nest within a termite nest that was overtaken by *taraqua* ants, fixed to a vine at 3 m above the ground • Habitat: *Várzea* forest • Igarapó Jaraqui, Rio Juruá, AM • 28/07/1993

Trigona cilipes (Fabricius, 1804)

Common names:
angelita, buhnide,
mehnôrá-kamrek.



95c

GENÉTICA
FM R. PRETO

Vila Nova do Tonantins
AM, Brasil, SA-19,68-3f. IX
22,23-I-1977, Camargo
M. Mazucato leg.

T. mazucatoe
Almeida, 1978
Det. Camargo, 2008





Nest within a termite nest on a dry tree trunk • Habitat: *Igapó*
• Carixeno, Rio Negro, AM •
08/07/1999

Nest within a live arboreal ant nest (*tachi*), in an orange tree •
Habitat: Dense, sub-montane forest, dissected relief • Mouth of the Rio Curicuriari, AM •
15-21/07/1980

Trigona cilipes



Nest within a live arboreal ant nest (*tachi*), in an orange tree •
Habitat: Dense, sub-montane forest, dissected relief • Mouth of the Rio Curicuriari, AM •
15-21/07/1980



Trigona crassipes (Fabricius, 1793)

Common names:
sombra-de-sucha,
fisi-wasi-wasi-oni.



U. Essequibo R.
Br. Guayana
XII-23-27

Acc. 36159
W. G. Hassler

PARATYPE

Trigona (Trigona)
hypogaea
variety robustior
H. F. Schwarz

T. (Trigona)
crassipes
(Fab., 1793)
Det. Camargo 1979

Trigona crassipes



Nest entrance in a cream nut tree cavity • Habitat: *Roçado, terra firme*
• Lago Uará, Rio Solimões, AM •
13/08/1993

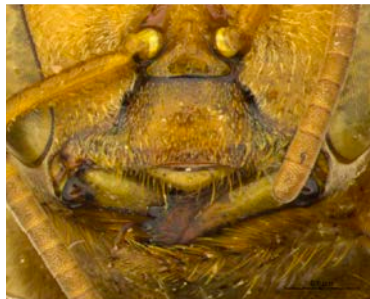


Nest within a live *fava* tree cavity, at 5 m above the ground • Habitat: *Terra firme* forest, 30 to 40 m high • Ipixuna, Purus, 42 km Tapauá, AM •
22/01/1986



Trigona dallatorreana Friese, 1900

Common names:
sicae-amarilla-
chica, kukraire, tu.



Obidos - Para
Brasil, I-1902
F. M. Oliveira.

*Trigona
dallatorreana*
Friese, 1900
Det. Moure, 1966

Trigona dallatorreana



Exposed nest, fixed to *marimari* tree branches
• Habitat: *Várzea* forest •
Paráiso, Rio Japurá, AM •
21/08/1993



Trigona dimidiata Smith, 1854

Visits Brazil
nut (*Bertholletia
excelsa*) flowers.



Rio Trairão. PA – Brasil
(50 km NE Gradaús)

SB-22,51°49' W,7°21' S
21,24-VII-79. Mazucato

T. dimidiata
Smith, 1854
Det. Camargo, 2008

Trigona guianae Cockerell, 1910

Common names:

txashkû-taxipa, djô.

Pollinates coconut (*Cocos nucifera*) flowers and visits Brazil nut (*Bertholletia excelsa*) flowers.



Belém - Para
BRASIL
VI - 1966
col. R. Zucchi

Trigona (Trigona)
fulviventris
Det. Moure - 1970





Nest within a dry trunk, with termites • Habitat: Mixed sub-montane forest, plateau and low plateaus, *campinas* • São Luís do Tapajós, PA • 14-17/01/1979



Underground nest • Habitat: Dense forest, lowlands, plateaus • Aruti, Rio Negro, AM • Data: 22-23/07/1980



Brood combs

Trigona hyalinata (Lepeletier, 1836)

Common names: xupé, abelha-brava, guaxupé, arapuá, timba-preta.

Pollinates guava (*Psidium guajava*), sunflower (*Helianthus annuus*) and cucurbits (*Cucurbita* spp.) flowers. Visits cotton (*Gossypium hirsutum*) and coffee (*Coffea arabica*) flowers.



Aragarcas
GO. - BRASIL

18-I-1971
Col. Camargo

6.a

T. (Trigona)
hyalinata
(4p., 1836)
Det. Camargo 1977

Trigona hyalinata



Exposed nest •
Habitat: Hillside,
with a very smooth
vertical layer of
sandstone • Alto
Parnaíba, 18 km SW,
MA • 23/01/1993



Trigona hypogea Silvestri, 1902

Common name:
mombuca-carnívora.



PARALECTOTYPE

"S. TERRESTRI,
nido, Cochipo"
11. IX. 1900"
Silvestri leg.

Trigona hypogea
Silvestri, 1902
Des. Camarao 1984

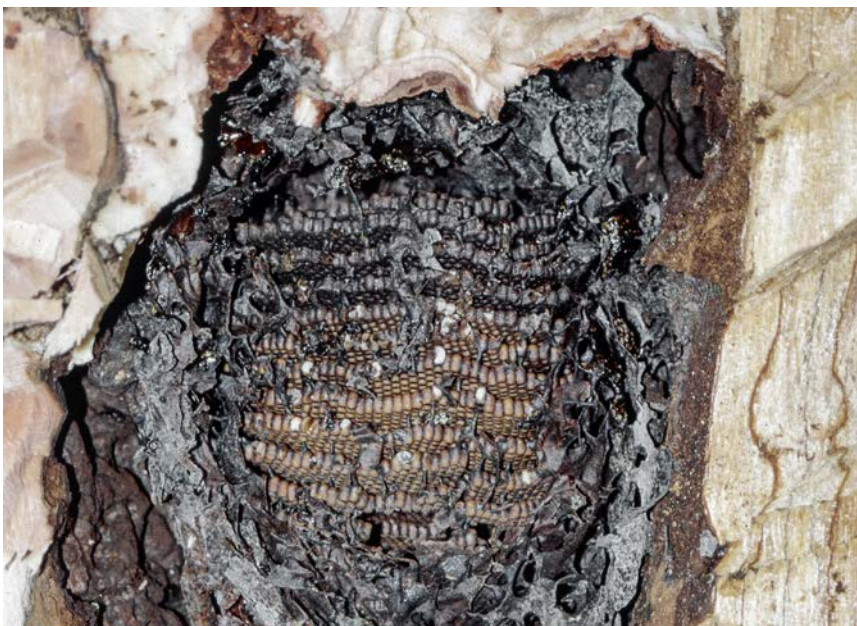


Nest entrance in a fallen, dead tree cavity • Habitat: Floodplain • Santa Maria, Itaituba, PA • 18-20/01/1979

Trigona hypogea



Nest in a fallen, dead tree cavity • Habitat: Floodplain • Santa Maria, Itaituba, PA • 18-20/01/1979



Nest within a live yellow mombin tree cavity • Habitat: *Terra firme*, pasture, forest fallen in 1990 • Bacururu, Rio Juruá, AM • 31/07/1993



Trigona pallens (Fabricius, 1798)



Common names: cutia-o-de-purga, colatakwa, tuu, myre, oloman-oni, lebi, redi-oni.

Pollinates murici (*Byrsonima crassifolia*), acapu (*Vouacapoua americana*), camu-camu (*Myrciaria dubia*), açai (*Euterpe oleracea*) and yellow mombin (*Spondias mombin*) flowers.

Visits cupuaçu (*Theobroma grandiflorum*) and muskmelon (*Cucumis melo*) flowers.



Bosque Madero
Araracuara Cta
Amaz. Colombia
0154-06-X-1988
Col. M. Torres 910016

Sobre Wottschae-
galia

Trigona pallens
Fabricius, 1798
Det. Camargo 1991

Trigona pallens

Nest within a termite nest in a hollow tree

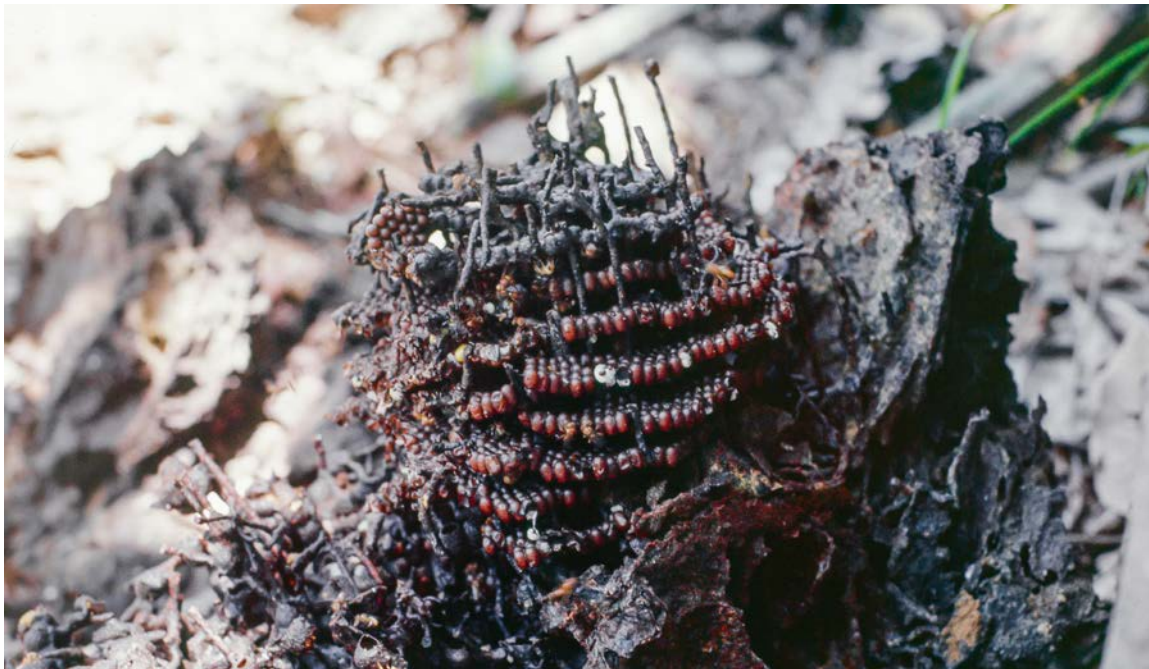
- Habitat: Tall forest, terra firme
- Tefé, AM
- 28/01/1977



Nest within hollow tree

- Habitat: Dense forest, lowlands
- Acanga, Rio Negro, AM
- 06-08/08/1980

Nest within a hollow tree •
Habitat: Dense forest, lowlands,
plateaus • Acanga, Rio Negro,
AM • 06-08/08/1980



Nest within a termite in a
hollow tree • Habitat: Tall
forest, *terra firme* • Tefé, AM
• 28/01/1977

Trigona pellucida Cockerell, 1912



Km 206 Rodovia
Cuiabá-Santa-
rem-Brasília
1975
Juliani leg

T. (Trigona)
gilipes pellucida
Ckfl., 1912
Det. Camarao 1979



Trigona recursa Smith, 1863

Common names: vamos-embora, feiticeira, vamo-nos-embora, puka-kam-mehn.

Pollinates camu-camu (*Myrciaria dubia*), bell pepper (*Capsicum annuum*) and strawberry (*Fragaria x ananassa*) flowers.

Visits cotton (*Gossypium hirsutum*) flowers.

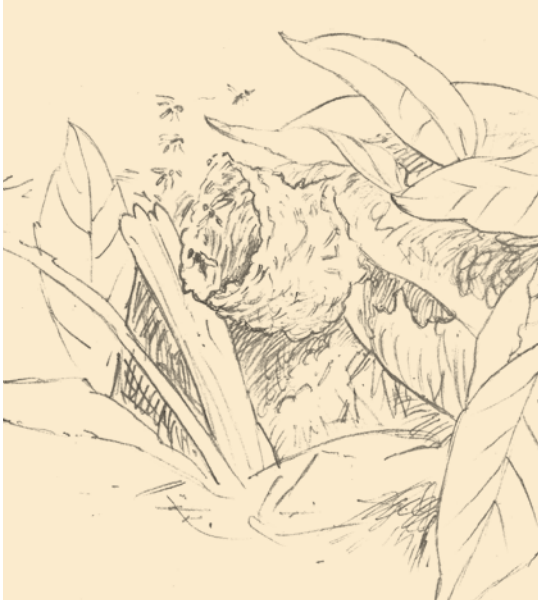


Mazucato

Estrela da Barra
MG. Brasil-7-VI-85
850718

T. recursa
Smith, 1863
região do tipo
Det. Camargo, 1999

Trigona recursa



Original drawing by J. M. F. Camargo; (Diário de Viagem Negro River, 1999).



Underground nest, at 90 cm below ground, without termites or ants • Habitat: *Roçado* close to tall, *terra firme* forest • Location: São Paulo de Olivença, AM • Data: 20/01/1977



Trigona spinipes (Fabricius, 1793)

Common names: irapuá, arapuá, abelha-de-cachorro, xupé-pequeno, urapuca, mbá-pý, carabozá, mehñykamrek.

Pollinates canola (*Brassica napus*), guava (*Psidium guajava*), cucurbits (*Cucurbita* spp.), umbu (*Spondias tuberosa*), muskmelon (*Cucumis melo*), yellow mombin (*Spondias mombin*), coconut (*Cocos nucifera*), macadamia nut (*Macadamia integrifolia*), annato (*Bixa orellana*), sunflower (*Helianthus annuus*), orange (*Citrus sinensis*), eggplant (*Solanum melongena*), mandarin orange (*Citrus reticulata*), onion (*Allium cepa*), strawberry (*Fragaria x ananassa*), chayote (*Sechium edule*), avocado (*Persea americana*), acerola (*Malpighia emarginata* and *M. glabra*), peach (*Prunus persica*), Barbados nut (*Jatropha curcas*), bell pepper (*Capsicum annum*), wild carrot (*Daucus carota*), pomegranate (*Punica granatum*), watermelon (*Citrullus lanatus*) flowers.



Massaranduba—
Blumenau, Brazil
Sept-Oct, 1935
Ac. 34235

Trigona (Trigona)
ruficornis (Fabr.)
Det. Schwarz

Trigona spinipes



Exposed nest • Habitat:
Coconut tree stand – Cerrado-
Caatinga transition (babassu
palm, carnauba palm, *cerrados*
• Nina Rodrigues, MA •
17/07/1982



Trigona truculenta Almeida, 1984

Common names:
sanharó, sanharão.



Barro do Geraes
MT., BRASIL
10.24.I.1977
Col. Camargo

T. (Trigona)
malthea
(Olivier, 1789)
Det. Camargo 1977

Trigona
truculenta
Almeida, 1984
Det. Camargo 1977

Trigona truculenta



Nest within a dead *apuí* tree,
strangling vine • Habitat:
Terra firme forest • Nazaré, Rio
Negro, AM • 16/07/1999



Trigona williana Friese, 1900

Common name:
kajawo-dawa.



Porto Velho
Rondonia - Brasil
12-22-X-1966
Col. Camargo

T. (Trigona)
williana
Friese, 1900
Det. Camargo 1979

Trigona williana

Nest entrance



Nest within a dry, rotten tree •
Habitat: *Capoeira, terra firme* •
Forte da Graça, Juruá River,
AM • 03/08/1993

Genus

Trigonisca Moure, 1950



Source: Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836. In: Moure JS, Urban D, Melo GAR (Orgs) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – online version.

Trigonisca dobzhanskyi (Moure, 1950)

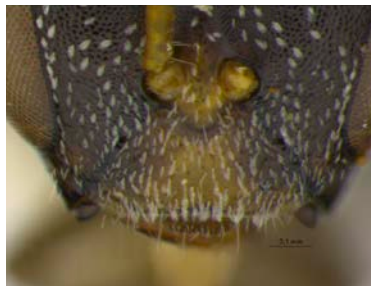


FRENCH GUIANA: Sinnamary
2.7 km SW; ORSTOM station
Road 8 May 1982
D. Roubik coll. No. 66

Trigonisca
dobzhanskyi
Moure, 1950
Det. Camargo 1982



Trigonisca fraissei (Friese, 1901)

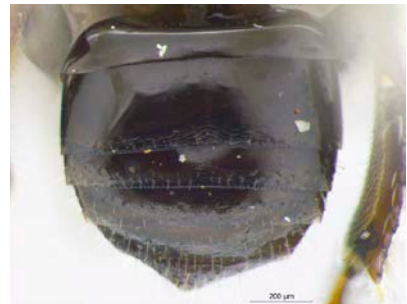


GENETICA
FM.R.PRETO

Aruti, R. Negro. AM.
Brasil - 22,23-VII-1980
SA-19,66°2'W, 0°19'S
Camargo, MaZucato leg

Trigonisca
fraissei
(Friese, 1901)
Det. Albuquerque, 1990

Trigonisca meridionalis Albuquerque & Camargo, 2007



P. de M. da Cruz MG
Brasil - 22-VII-1988
44°23'W 15°36'S
M. MaZucato leg

HOLOTYPE
Trigonisca meridionalis
Albuquerque & Camargo, 2007

Trigonisca variegatifrons Albuquerque & Camargo, 2007



LAGO AGUA FRIA, PA.
Rio Trombetas - BRASIL

SA.21-X-C.56°51'W,1°25'S
13-15,II-1979. Camargo

HOLOTYPE
Trigonisca
variegatifrons
Albuquerque, 1990

Trigonisca vitrifrons Albuquerque & Camargo, 2007

Visits Brazil nut
(*Bertholletia excelsa*)
flowers.



LAGO AGUA FRIA, PA.
Rio Trombetas - BRASIL

SA.21-X-C,56°51'W,1°25'S
13-15,II-1979. Camargo

HOLOTYPE
Trigonisca
vitrifrons
Camargo, 1990



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