



Species redescription and nest architecture of *Plebeia flavocincta* (Hymenoptera: Apidae: Meliponini)

Ulysses Madureira MAIA^{1,2}, Rafael Cabral BORGES^{1,2},
José Eustáquio dos SANTOS-JÚNIOR³, Victor Hugo Pedraça DIAS⁴,
Airton Torres CARVALHO⁵, Vera Lucia IMPERATRIZ-FONSECA⁶,
Guilherme Corrêa de OLIVEIRA², and Tereza Cristina GIANNINI^{1,2}

¹ Instituto de Ciências Biológicas, Universidade Federal Do Pará, Belém, Brazil

² Instituto Tecnológico Vale, Belém, Brazil

³ Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

⁴ Instituto de Assistência Técnica E Extensão Rural, Mossoró, Brazil

⁵ Unidade Acadêmica de Serra Talhada, Universidade Federal Rural Do Pernambuco, Serra Talhada, Brazil

⁶ Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

Received 25 January 2022 – Revised 12 July 2022 – Accepted 9 September 2022

Abstract – Bees are important insects both environmentally and economically. Despite this, most bee species are poorly characterized regarding their morphology and nesting habits, which are relevant characteristics for planning management and conservation. *Plebeia flavocincta* is a stingless bee species that occurs in the Northeast region of Brazil and there is little knowledge about its morphology and nesting biology. Here, we morphologically characterize *Plebeia flavocincta* workers from 54 colonies and use seven colonies to describe the structure of the species' nest. All nests were found in seasonally dry forest areas in different substrates, namely, hollow of native trees, wall, post, and wooden boxes. The structure of the species' nest was detailed in terms of the number, shape, and area of the combs; brood cell size; size of food pots; nest size; and honey volume. *Plebeia flavocincta* is found in both natural and urban environments. The structure of the nest of *Plebeia flavocincta* is similar to that found in other species of the same genus. This is the first nest diagnosis study of the species. In addition, by establishing morphological data to recognize *Plebeia flavocincta*, this study provides useful information for management and conservation plans for the species.

Caatinga / Morphological characterization / Nest structure / Stingless bee / Beekeeping

1. INTRODUCTION

The stingless bees (Meliponini, sensu Michener 2007) make up the most diverse group of eusocial bees (Michener 2007). In the Neotropics, 417 species have been described (Camargo and Pedro 2013), and about 259

species can be found in Brazil (Camargo and Pedro 2013). Bees are of both ecological and economic importance (Klein et al. 2007). Ecologically, pollination is an essential function for the maintenance of life on the planet, as most flowering plants depend on bees for their reproduction (Ollerton et al. 2011). On the other hand, economically, bees are important pollinators of agricultural crops (Klein et al. 2007; Giannini et al. 2015; Campbell et al. 2018), in addition to being a source of nutrition and income for traditional communities through their breeding and

Corresponding author: U. M. Maia,
ulymm86@hotmail.com
Manuscript editor: James Nieh

management (Jaffé et al. 2015; Potts et al. 2016; Hill et al. 2019). Some stingless bee species can be used in the production of bee products such as honey, pollen, wax, and propolis. They may also be kept with a cultural interest (i.e., as a hobby), focusing on breeding and selling nests, or for renting the nests, aiming at providing crop pollination services (Cortopassi-Laurino et al. 2006; Jaffé et al. 2015; Potts et al. 2016; Hill et al. 2019). For ensuring a safe and environmental friendly commercialization of stingless bees' nests (Santos et al. 2022), a broad taxonomic, biogeographic, behavioral, and ecological knowledge of each focus species is required (Freitas et al. 2009), in order to prevent pervasive side effects (e.g., biological invasions, hybridization).

The difficulty in stingless bees' identification at species level is a recurrent problem; in several cases, it is mainly related to the fact that many species are very closely related, with minor differences to separate them, in addition to the lack of a detailed original description, and identification keys (Roubik 2013). Thus, the taxonomic impediment ends up triggering other impediments. If the species cannot be correctly identified, it is not possible to attribute a geographic distribution range, behavioral and ecological information to it. Knowing the natural limits of occurrence of managed species is extremely important to prevent the management of these species to exotic habitats, which would result in a process of biological introduction and possible species hybridization (Wiens 2011; Byatt et al. 2016; Santos et al. 2022). Understanding the patterns of nest architecture is complementary to taxonomic decisions, and to management techniques that can be developed for each species, supporting the maximum possible production, as well as the maintenance of nests in the long term. *Plebeia* Schwarz, 1938 is a diverse genus of stingless bees (~45 described species), and widely distributed, from Mexico to Argentina. The genus does not have an updated identification key and needs a taxonomic review to determine the main differences between the valid taxa, as well as to redescribe the taxa for which only brief descriptions are available (Silveira et al. 2002; Camargo and Pedro 2013). In Brazil, about

20 of the 45 described species for the genus are known (Pedro 2014) and they are commonly used by beekeepers, mainly for honey production (Jaffé et al. 2015). Given the difficulty in identifying *Plebeia* bees at species level, nest characteristics may provide a strong support for identifying species in this genus (Camargo and Moure 1988; Witter et al. 2007).

Among the *Plebeia* species used by beekeepers, *Plebeia flavocincta* (Cockerell 1912) has a restricted distribution, mainly in the semi-arid areas of Northeastern Brazil (Maia et al. 2020). This bee species has a small size (~4.5 mm), and is locally known as “mosquito” or “jati bee.” Despite its size, *P. flavocincta* is among the most managed stingless bees in the Caatinga (together with *Melipona subnitida* Ducke 1910) (Maia et al. 2015; Felix and Freitas 2021). It is an important floral visitor to native plant species in the semi-arid region, interacting with more than 50 wild plant species (Imperatriz-Fonseca et al. 2017). The honey produced by *P. flavocincta* (even that in small quantities) is highly appreciated and valued by the local people as food and medicine, as it happens with several other stingless bee species (Potts et al. 2016). In fact, the honey produced by *P. flavocincta* has been shown to present antifungal properties (Silva et al. 2015) and the geopropolis presents antibacterial and wound-healing properties (Silva et al. 2016).

Despite the importance of this native stingless bee, the description of *P. flavocincta* remains poorly informative and its nest has not been described yet. Thus, this work aims to redescribe *P. flavocincta* based on morphological characters. Description will be based on the type specimen and specimens sampled throughout its distribution range, also adding new geographic records. The objective also includes detailing the architecture of *P. flavocincta* nests from natural (i.e., tree trunks) and anthropogenic nesting sites (i.e., associated with anthropogenic constructions), to provide information for its characterization and support species identification. This knowledge will contribute to the sustainable management activities and will provide support for decision-making in the context of conservation strategies,

aiming to protect the ecosystem service (pollination of plant species in the Caatinga biome) provided by native bees in Brazil.

2. MATERIAL AND METHODS

2.1. Species redescription

In this study, we examined 108 specimens of *Plebeia flavocincta* from the bees of the semi-arid collection of the Federal Rural University of the Semi-Arid (ASA-UFERSA). These specimens belonged to 54 different nests (two specimens per nest) distributed in 16 municipalities in the Northeast region of Brazil (Supplementary Material). We examined the type material (photographs) of *P. flavocincta* from the National Museum of Natural History (USNM), Entomological Collection, Smithsonian Institute, Washington DC, USA. For species redescription, we used all examined specimens (including the type); for measurements, we used only the examined specimens from ASA-UFERSA (type not included). The terminology for external morphology in this study follows that of Michener (2007). We examined the specimens on a Zeiss Stemi 2000-c stereomicroscope equipped with a micrometric reticle used for measurements. Karolyn Darrow from the USNM provided photos of the type specimen. Species distribution is based on sampled and examined material (for further information, see Maia et al. 2020).

Study of nests The nests' description was carried out in the municipalities of Caucaia (CE) (03°69'63" S, 38°74'56" W) and Mossoró (RN) (05°11'16" S, 37°20'38" W), both in the Northeast region of Brazil. The study of the nests' biology and architecture was carried out from January to February 2021. The municipality of Caucaia is characterized by deciduous vegetation associated with coastal vegetation, with an average temperature of 27 °C and an average rainfall of 1243 mm per year (Funceme 2019). According to the Köppen climate classification, the climate of Caucaia is tropical and semi-humid. The municipality of Mossoró is characterized

by deciduous vegetation, typical of semi-arid areas, with an average temperature of 27.5 °C (Carmo Filho et al. 1991) and an average rainfall of 670 mm per year (Santos et al. 2014). According to the Köppen climate classification, Mossoró's climate is hot and dry.

For the study of nests, we analyzed seven nests in total, six located in Mossoró and one in Caucaia. Measurements were taken from the entrance hole of the nest (diameter) and the circumference of the trunks (when in trunks, two out of seven nests). To open, visualize, and study the nests' internal structure and architecture inside the trunks, an ax, sledgehammer, and steel chisel were used to gain access to the brood chambers. Only one nest was located inside a wall and was opened using a sledgehammer and a steel chisel. After opening the nests, the width and length of the brood chamber were measured. The brood disks and the number of brood cells present in the nest were counted. All brood comb, six brood cells, the royal cells, and six food pots were measured. Food pots were counted and inspected (for pollen and honey). The amount of honey in each nest was measured. When possible, a description of the materials used by the bees and the internal structure of the nests was performed.

For the measurements, a pachymeter and/or a measuring tape was used. The content of honey pots was extracted and measured with 3-mL syringes without needles. The population size of each nest was inferred through the Eq. (1.5*X), where X represents the total number of brood cells counted, following Ihering (1932).

3. RESULTS

Plebeia flavocincta (Cockerell, 1912) Redescription. Female, worker (Figure 1). Body length approximately 4.5 mm; head 1.2 times wider than long (width 1.6 mm, length 1.4 mm) (Figure 1A); minimum distance between eyes 0.8 mm; distance at ocular sinus 1 mm; clypeus concave, apical margin straight, 2.3 times wider

than long (width 0.7 mm, length 0.3 mm); malar space nearly obsolete, about 0.2 times the width of the mandible basis; antennal scape elongated (7.5 times longer than wide), nearly cylindrical, antennal apex as wide as base; eye about 2.2 times longer than its maximum width, in lateral view, nearly as wide as maximum width of gena; posterior ocelli widely separated, distance between ocelli 2.2 times the ocelli diameter; oculo-orbital distance, in dorsal view, 0.75 times

distance between posterior ocelli; mesoscutum about as long as wide, intertegular distance 1.1 mm; scutellum more than 2 times wider than long; fore wing length 3.5 mm, maximum width of Terga 2 1.6 mm.

Integument surface Overall integument smooth and shiny (Figure 1B). Piligerous and conspicuous punctuation on clypeus, frons, pronotum, mesoscutum, and scutellum. Frons, pronotum,

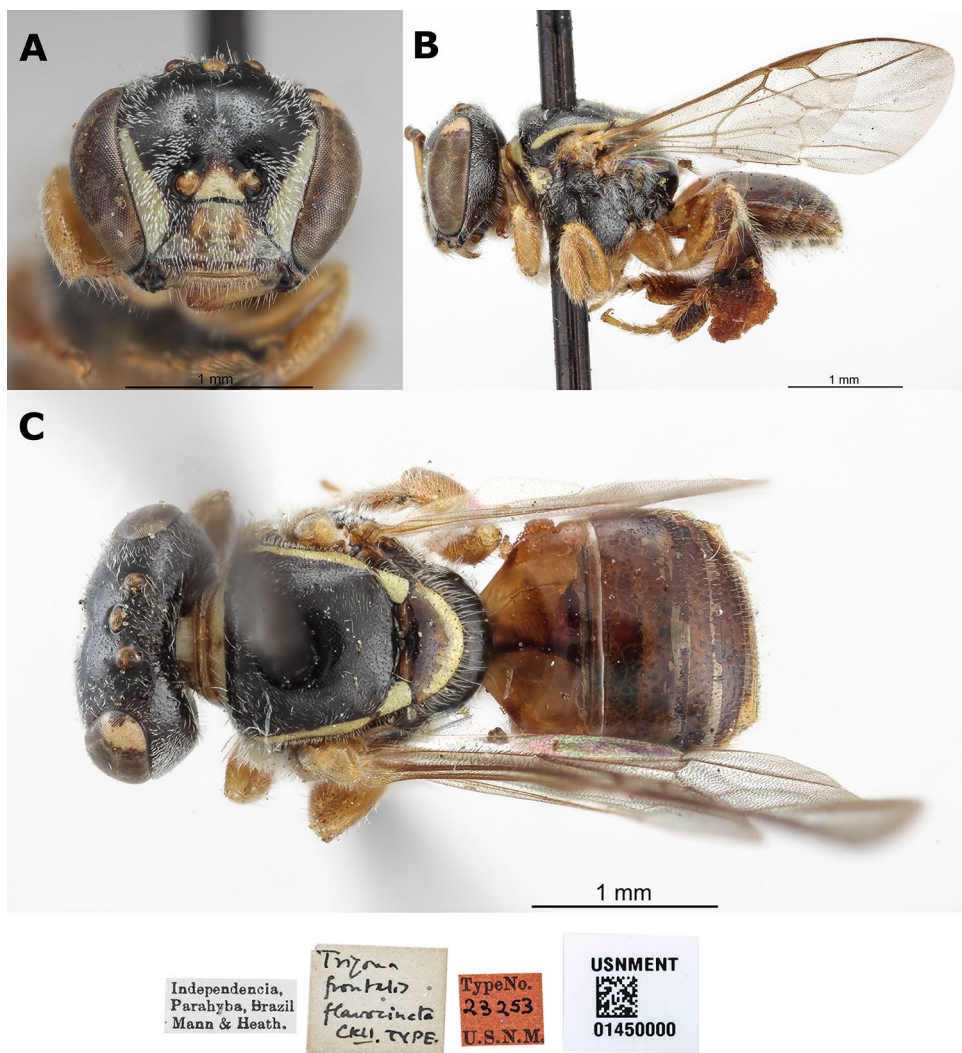


Figure 1. Type specimen of *Plebeia flavocincta*. (A) Frontal view. (B) Lateral view. (C) Dorsal view and specimen labels. Photos by Karolyn Darrow from Smithsonian Institution.

and mesoscutum with granulate punctures, those on frons and mesoscutum separated by more than one diameter, those on pronotum bigger and separated by less than their diameter.

Pubescence Predominantly covered by white pubescence, except for light brown setae on inner surface of tarsi and brown microtrichiae on wings. Eyes with short, nearly indistinguishable setae. Head and lateral portion of mesepisternum with conspicuous decumbent finely plumose hairs; longer (0.1 mm) and erect setae on the ventral portion of clypeus, mandibles. Long setae (0.2 mm) between posterior ocelli and on posterior portion of the head (around occiput). Long (0.25 mm), erect and finely plumose setae on anterior margin of mesoscutum, those on lateral margins shorter (0.1 mm), disc of mesoscutum covered by fine, decumbent, and simple setae. Long setae on posterior margin of scutellum (0.25 mm). Legs with long and erect hairs (0.06–0.25 mm). Fine pubescence on abdomen. T4–T6 with long (0.15 mm) and erect hairs, those on ventral portion restricted to the central areas.

Color Integument black and yellow (Figure 1C). Upper portion of frons, posterior portions of the head, mesoscutum (except lateral margins), pronotum (except pronotal carina), mesepisternum, metanotum, propodeum black. Clypeus, inner orbital margins (lower two-thirds), ventral portion of antennal scape, mandibles (except for posterior margin and teeth), lateral margins of mesoscutum, scutellum, axilla, ventral portion of abdomen, fore and mid legs, hind coxa, and throcanther yellow. Upper portion of antennal scape, pedicel, flagella, posterior margins of mandibles (and teeth), upper portion of abdomen, hind legs brown.

Male Unknown.

Type material Worker holotype “Independencia, Parahyba, Brazil, Mann and Heath, Type No. 232253 U.S.N.M., USNMENT 01,450,000”.

Examined material See supplementary material.

Geographical distribution Brazil, Alagoas (Água Branca), Bahia (Canudos, Casa Nova, Glória, Mucururé, Tucano), Ceará (Aiuaba, Aracoiaba, Baturité, Capistrano, Crato, Fortaleza, Mulungu, Ubajara, Poranga), Paraíba (Bananeiras, Guarabira, João Pessoa), Pernambuco (Buíque, Cabo de Santo Agostinho, Caruaru, Igarassu, Itaquitanga, Moreilândia, Recife, Triunfo), Rio Grande do Norte (Apodi, Assu, Galinhos, Jandaíra, Jardim do Seridó, Martins, Mossoró, São Miguel, São Paulo do Potengi), Sergipe (Canindé de São Francisco).

Notes The type locality, Independencia, has changed and the municipality is currently called by its original name Guarabira, since 1977.

Description of nests The measurements of *P. flavocincta*'s nest are presented in Table 1. The trunk hollows where the nests were found belong to *Commiphora leptophloeos* (Mart.) J.B. Gillett (Burseraceae).

3.1. Nest architecture

3.1.1. Nest entrance

The nest entrance was a circular and simple hole with a diameter ranging from 0.40 to 0.70 cm (0.53 cm on average) (Figure 2A). No debris (e.g., clay particles, gravel, leaves, kindling, and sawdust) was observed in any of the nests. However, the nest entrance was covered by a layer of wax and resin. From the inside of the nest, four to five workers monitored the entrance during daytime, exposing only their heads (Figure 2B). During the night, the workers close the entrance orifice, apparently with a layer of wax and resin (Figure 2C).

3.2. Tunnel to the nest cavity

The length of the access tunnel depends on the thickness of the nest wall and the shape of the duct. We observed straight tunnels directly into



Figure 2. Entrance hole of the *Plebeia flavocincta* nest in a (A) trunk of *Commiphora leptophloeos*, (B) wall, and (C) manmade wooden hive with emphasis on the entrance hole closed at night. Photos: UMM.

the brood chamber and tunnels with curves close to the inner cavity wall of the nest. The length ranged from 5 to 6.5 cm with a mean value of 5.9 cm. In general, the tunnel is reinforced with a harder layer of cerumen (wax and propolis) and opens in the brood chamber of the nest

(Figure 3). Trunk nests can have longer tunnels due to the distance from the entrance hole to the nest chambers. These tunnels may not be covered with cerumen. Nests in which the entrance hole is closed to the nest chambers have a shorter and visible tube of cerumen.

3.3. Nests

The nests were observed in four types of cavities (manmade wooden boxes, fence posts, wall bricks, and trunks). The studied nests did not completely occupy the cavities where they were inserted, as they had batumen layers (geopropolis) to delimitate the extension of the nest area. Geopropolis is almost pure, with the presence of sand and clay. The cavities had a larger volume than the nest. The shape of the nest varied according to the shape and size of the cavity. In native tree trunk nests, the length of the nest is greater than the width of the cavity. In the wall nest, the access to the holes in the brick used to build the nest varied. This nest had a brood chamber separated from the food storage chamber. However, it was possible to observe pots of pollen near the brood area, a common feature in stingless bees. The length of the nest ranged from 12 to 73 cm, with an average of 43 cm and the nest volume ranged from 657 to 2736 cm³, with an average of 1644 cm³.

3.4. Brood area

The length of the combs ranged from 3.9 to 18.0 cm. The combs are shaped like complete

horizontal disks (Figure 4). The diameter (width) of the comb ranged from 1.4 to 6.0 cm. The number of brood combs ranged from 4 to 18. A colony with smaller brood discs does not necessarily have fewer brood cells, as small discs may be spread out in narrower cavities within the brood chamber. Several pillars made of cerumen support the combs. The brood cells had an average height of 0.4 cm and an average diameter of 0.3 cm. The height of a royal cell was 0.6 cm, that is, 50% larger than a worker brood cell (Figure 5). Royal cells are built at the edges of the comb. We observed that several brood cells were built at the same time. The presence of “trochoblasto” was observed in two nests, that is, the remaining background of brood cells whose walls had been demolished after the adult bee emerged. The brood envelope was observed in all nests. It consisted of one to two layers of soft wax in colors ranging from pale yellow to light brown.

3.5. Food pots

Food pots are usually located deeper in the nest. They form a solid mass, but in some cases, they are spread around the brood



Figure 3. Brood area of the *Plebeia flavocincta*, with detail showing a nest entrance chamber, which was built into a wall.



Figure 4. Nest of *Plebeia flavocincta* in the trunk of *Commiphora leptophloeos* with emphasis on the combs in the shape of horizontal disks.

chamber. The pots near the brood area were pollen pots. The shape of the food pots was oval (Figure 6). Pollen and honey pots are similar. The outer walls of the pots were thick and

dark brown; the walls between the pots were thin and sometimes cracked, connecting one to the other. The height of the food pots was, on average, 1.29 cm, ranging from 0.9 to 1.7 cm.

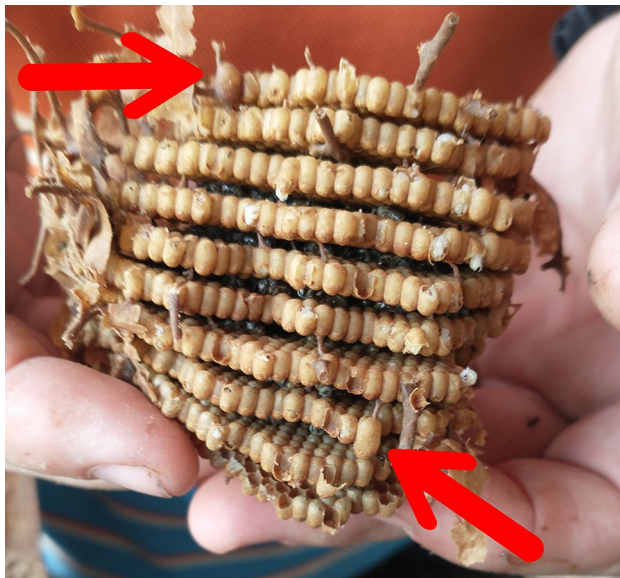


Figure 5. Size of two real cells of *Plebeia flavocincta* compared to other brood cells around it.

The mean volume was 0.52 mL/pot and 35 mL/colony. The mean stored pollen weight could not be measured.

3.6. Propolis deposits

Both in the brood chamber and the food storage chamber, small deposits of dark-colored propolis were formed. The layer has a hard and sticky consistency. The shape of the deposits is round, like propolis pellets. The number of propolis deposits ranged from one to four.

3.7. Garbage

In the free space between the solid mass of food pots, at the bottom of the nest, in the space between food pots, and sometimes close to the brood area, we detect garbage deposits (decomposing materials), probably discarded by the workers. We did not detect the presence of dead bees or other arthropods, although this has been commonly reported by beekeepers of *P. flavocincta*.

3.8. Population

The estimated population, including young and adults, ranged from 270 to 3340 individuals, with a mean value of 1817. We did not observe the presence of males during the nests' observations, as they were not in the swarming period. It was possible to find, in two nests, queens imprisoned in special cerumen chambers twice the size of a food pot (Figure 7). In all observed nests, bees did not present aggressive behavior towards the observers.

4. DISCUSSION

In this study, we increased the available morphological description information from specimens of *P. flavocincta* collected along with its geographic range. With this new information, it was possible to delimit the species more precisely. Thus, even collected in a variety of environments, all specimens corresponded to the same taxon under study. We proposed to



Figure 6. Compact mass of food pots from a nest of *Plebeia flavocincta* located in a wall.



Figure 7. A special wax chamber where it was possible to find a trapped queen.

Table I. Measurements of the seven nests of *Plebeia flavocincta* from two municipalities in Northeastern Brazil (Caucaia and Mossoró)

Variables	Unit	Variation	Mean	Standard deviation
Circumference (trunks)	cm	33.0–97.0	60.00	33.15
Hole diameter	cm	0.4–0.7	0.53	0.11
Inner tube size	cm	5.0–6.5	5.90	0.55
Nest length	cm	12.0–73.0	43.14	21.65
Nest cavity width	cm	3.0–8.0	5.42	1.86
Width of the nest wall	cm	2.0–11.0	4.64	3.02
Number of food pots	un	30.0–130.0	67.83	40.13
Volume of honey pots	mL	0.4–0.7	0.52	0.11
Size of food pots	cm	0.9–1.7	1.29	0.22
Breeding area size	m ²	5.46–96.0	52.48	31.83
Number of brood discs	un	4.0–18.0	11.29	5.19
Number of casing layers	un	0.0–1.0	0.71	0.49
Brood cell height	cm	0.3–0.5	0.40	0.06
Brood cell width	cm	0.3	0.30	0.00
Presence of real cells	un	0.0–4.0	1.29	1.38
Size of actual cells	mm	0.6	0.60	0.00
Presence of imprisoned queen	un	0.0–2.0	0.43	0.79
Pot area volume	m ³	41.0–390.0	161.82	154.20
Number of garbage dumps	un	2.0–4.0	2.67	1.15
Number of propolis deposits	un	1.0–4.0	2.17	1.17
Estimated honey production	mL	15.6–67.6	35.27	20.87
Number of brood cells to be born	un	180–2227	1211.57	699.87
Estimated population	un	270.0–3340	1818	1049.80

characterize our model species and to facilitate identification in future studies. We also describe for the first time the structure of their nests as well as estimate their population size. The species shares numerous morphological and nesting characteristics with the genus *Plebeia*.

Superficially, it resembles *Plebeia phrynostoma* Moure, 2004 by presenting a similar coloration, pubescence, and integument sculpture. However, *P. flavocincta* differs mainly in the body size (*P. phrynostoma* being smaller), the color of the head (marginal orbit with yellow stripes not parallel and smaller in *P. flavocincta*), and the color of pronotum (*P. flavocincta* with pronotum entirely dark brown). The nest entrance also differs, as *P. flavocincta* presents a simple and circular entrance, while in *P. phrynostoma* the entrance is elongated and narrow, like a slit (Moure 2004). In addition, they are not co-occurring species, since *P. phrynostoma* is restricted to the Southeastern Brazil (Minas Gerais and Espírito Santo states) (Moure 2004), while *P. flavocincta* is largely spread throughout the semi-arid portions of the Northeast region in Brazil (from Ceará to Bahia) (Maia et al. 2020).

Most species of stingless bees build their nests in preexisting cavities, usually in the hollows of living trees (Nogueira-Neto 1997). Nests can also be found in other cavities, such as in anthills, termite mounds, and in the ground (Roubik 2006). The presence of *P. flavocincta* nests in different substrates, such as native or exotic tree trunks (Ribeiro and Taura 2019) and preexisting unnatural cavities (walls), suggests that the species can adapt to different substrates, in both urban and rural areas. We did not observe adornments in the nest entrance, but it is known to beekeepers that *P. flavocincta* sometimes has an entrance tube that is lighter in color and smaller in diameter than the tube observed in species, for example, of the genus *Scaptotrigona* Moure 1942. The workers close the nest entrance during the night with wax and resin, probably to avoid the invasion of natural enemies or to facilitate the control of the internal temperature of the nest (when the environment temperature is usually lower). The inner inlet tube is fixed to the cavity wall and is coated with a layer of cerumen,

probably to isolate the air inlet and control the internal temperature of the nest. Several workers can be found in the tube, also seeking protection against natural enemies. This is a common trait in stingless bees (Suka and Inoe 1993).

In the brood area, the layers of involucrum also have the function of maintaining a constant temperature inside the nest and retaining the heat produced by the brood's metabolism (see Wille (1983) for a description of this function). In *Plebeia remota* (Holmberg, 1903), the involucrum is present only during the period of interruption of the construction of brood cells and its functionality is to offer survival conditions during the winter (Ribeiro et al. 2003). Other species from the Southern region such as *Plebeia wittmanni* Moure and Camargo, 1989, *Plebeia julianii* Moure, 1962, and *Plebeia nigriceps* (Friese, 1901) do not have an involucrum (Witter et al. 2007). According to Wittmann (1989), *P. wittmanni* does not regulate the internal temperature of the nest properly and, as it nests in rocks, this may explain the absence of involucrum, since the properties of the rocks can contribute to the maintenance of the internal temperature of the nest. In *P. flavocincta*, not all nests presented involucrum layers. For this species, the casing layers are often spaced and irregular and do not cover the entire brood area. Beekeepers have already observed that this bee often covers the entire brood area with one or two layers of casing and that in other nests there is no casing. An explanation for the presence or absence of involucrum in *P. flavocincta* could be due to the location of the hives (wooden box plus the nest) and the thickness of the wall or cavity of the nest. Some hives may be better located in shaded areas or with differences in the wall thickness of the substrate in which they are located (thickness of the trunk wall or rational box, for example) causing a differentiation in the internal temperature between the hives. Thus, a meliponary can have hives with presence and others without an involucrum.

Plebeia lucii Moure, 2004, *Plebeia tica* (Wille 1969), *Plebeia minima* (Gribodo, 1893), *Plebeia moureana* Ayala, 1999, *Plebeia grapiuna* Melo and Costa, 2009 and *Plebeia franki* (Friese, 1900) are species already known that build

cells in the shape of bunches. Werneck (2016), studying the phylogeny of the *Plebeia* clade, received specimens from the State of Ceará donated by prof. Dr. Breno Magalhães de Freitas from the Federal University of Ceará (UFC). Although not identified, they were probably *P. flavocincta* (Breno Magalhães, personal communication). Thus, *P. flavocincta* belongs to the “*droryana* group,” together with *Plebeia droryana* (Friese, 1900), *P. phrynostoma*, *Plebeia saiqui* (Friese, 1900), and *Plebeia emerina* (Friese, 1900). Like *P. flavocincta*, all known species of the *droryana* group build their brood cells in horizontal disc combs. The royal cells are built on the comb margins, a typical position for most stingless bees (Nogueira-Neto 1997). *Plebeia flavocincta* also imprison virgin queens inside the special wax chamber, a way to avoid the colony’s death in case of a possible loss of the fertilized queen. *P. flavocincta* is the northern-most species within the “*droryana* group,” occurring mainly in Northeast Brazil. In addition, the only comb-building species to occur in the Northeast Brazil are *P. droryana* (in Bahia), *P. minima* (Maranhão), and *P. flavocincta* (from Ceará to Bahia).

Our results show a wide variation in the population size of the species. This variation can be explained by the difference in the substrates used for nesting. Nests with larger brood areas were more populated and stronger. This was also noticed for the number of food pots. Furthermore, the flight activity of *P. flavocincta* reflects the status within the nest, mainly in terms of food stock and population size (Barbosa et al. 2020). A strong colony of *P. flavocincta* can be quite populous when compared with *P. remota* (Alves et al. 2009) and with species of the genus *Melipona* Illiger, 1806 (and also *P. minima*, see Leão 2019). However, as noted by Leão (2019), the estimation of population size by formulas requires caution as the number of bees could not be counted. It is noteworthy that the species does not have diapause such as *Plebeia saiqui* (Pick and Blochtein 2002) nor reproductive diapause such as *P. droryana* (Santos et al. 2016) and *P. remota* (Ribeiro et al. 2003), species with distribution in the south and Southeastern Brazil. These differences may be related to the contrasting climatic conditions between those regions

and the Northeast. Since *P. flavocincta* does not have aggressive behavior, it can be bred in urban environments, both for the production of by-products (pollen, honey, and geopropolis), as well as for pollination in greenhouses or as a pet.

The estimated mean production of stored honey for *P. flavocincta* was 35 mL/colony. Honey, even in small quantities, is highly appreciated and considered medicinal by the local population. A liter of honey can cost around 50 dollars (USD), which is currently equivalent to one-fifth of the Brazilian minimum wage. However, honey is mostly used for consumption and is hardly traded, as there is no legalization of trade and the annual production of a box is small. A hive is also an object of trade in Brazilian meliponiculture (Cortopassi-Laurino et al. 2006; Santos et al. 2022). The value of a jati bee nest today costs around 40 dollars (USD). The propolis present in the nests and normally used by workers to seal gaps and to defend against other invading insects also has the potential to be a product derived from the nest mainly due to its pharmacological properties (Sanches et al. 2017). Beekeeping and management of *P. flavocincta* can be an important activity for a source of extra income, in addition to promoting species conservation and the maintenance of pollination services for native plants and crops.

Final considerations The Caatinga covers most of Northeastern Brazil and is at high risk of desertification due to several factors, such as deforestation and climate change (Santana 2007). In general, the Caatinga areas are characterized by deciduous vegetation that is regularly cut and used for firewood (Araújo Filho et al. 2018). The absence of trees is a problem for stingless bees since many of them build their nests in the hollow of living trees (Nogueira-Neto 1997). The *P. flavocincta* has already been found nesting in five tree species present in urban areas (four exotic and one native) in the State of Pernambuco (Ribeiro and Taura 2019) and in a native tree species in the State of Paraíba (Martins et al. 2004). During the mobilization for the beginning of this study, we consulted more than 100 beekeepers and we found that few breeders still have *P. flavocincta* in trunks. However, cutting

down trees to remove stingless bees is considered a crime under Brazilian law. The low number of nests in tree holes among breeders is possibly also associated with the teaching of good practices aimed at the preservation of stingless bees. In addition to developing good practices, bee breeding and physiology studies have been conducted by the Federal Rural University of the Semi-Arid (UFERSA) and by the Assistência Técnica e Extensão Rural from Rio Grande do Norte (EMATER/RN), in collaboration with the Associação dos Meliponicultores e Meliponicultoras Potiguar (AMEP) during the last five years. These initiatives are helping not only to conserve the environment but also to improve the management and protection of stingless bees.

5. CONCLUSION

This is the first study to describe in more detail specimens of *P. flavocincta* throughout its geographic range. Detailed descriptions and characterization of the nests contribute to the fact that the species, in addition to being accurately identified, can be managed for crops and nutrition and income production through meliponiculture, helping in their conservation and sustainable use. The architecture of *P. flavocincta* nests is similar to other species of the genus. This species is capable of occurring in anthropized areas, as it builds its nests in various types of preexisting cavities, including exotic trees and unnatural substrates such as walls. The wide range of occurrence of *P. flavocincta* throughout the Caatinga biome added to its docility, contributes to the species being easily managed in rational boxes in different locations, within its natural distribution area, for the production of honey and pollen, pollination, or as a pet. The species is also a good model for breeding, management, pollination, and conservation studies.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-022-00968-9>.

ACKNOWLEDGEMENTS

We thank the Fundação Amazônia de Amparo a Estudos e Pesquisas—FAPESPA (doctoral grant, Public Notice 005/2016), the Instituto Tecnológico Vale (ITV (project grant RBR000603.81), the Universidade Federal de Minas Gerais (UFMG) (curator Fernando Silveira) and the Universidade Federal Rural do Semi-Árido (UFERSA) for logistical support during part of the study. We also thank prof. Jeferson Coutinho, Juliana Galaschi Teixeira, Marcia de Fátima Ribeiro, William Sabino, Felipe Andres Leon Contrera, Charles Fernandes dos Santos, and Orlando Tobias for suggestions and comments. We also thank Karolyn Darrow of the Smithsonian Institution for the photos and the stingless bee beekeepers (Devanir Silva, Seu Dantas, Claudio Rogério de Souza, and Aurélio Barros-Júnior) for opening the nests and for important field information.

AUTHOR CONTRIBUTION

UMM, GCO, and TCG conceived the ideas. UMM, VHPD, and RCB collected data. UMM designed the methodology. UMM, ATC, JESJ, and VLIF analysed the data; all authors contributed to drafting the manuscript.

FUNDING

This work was supported by Fundação Amazônia de Amparo a Estudos e Pesquisas—FAPESPA (doctoral grant for UMM, Public Notice 005/2016) and the Instituto Tecnológico Vale (ITV (project grant RBR000603.81).

DATA AVAILABILITY

All relevant data are within the manuscript and its Supporting Information files.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

REFERENCES

- Alves DA, Imperatriz-Fonseca VL, Santos-Filho PS (2009) Production of workers, queens and males in *Plebeia remota* colonies (Hymenoptera, Apidae, Meliponini), a stingless bee with reproductive diapause. *Genet Mol Res* 8(2):672–683. <https://doi.org/10.4238/vol8-2kerr030>
- Araújo Filho RN, Freire MBGS, Wilcox BP, West JB, Freire FJ, Marques FA (2018) Recovery of carbon stocks in deforested caatinga dry forest soils requires at least 60 years. *For Ecol Manag* 407:210–220. <https://doi.org/10.1016/j.foreco.2017.10.002>
- Barbosa ABS, Meneses HM, Rosa FL, Freitas BM (2020) Flight activity of the stingless bee *Plebeia* aff. *flavocincta* in tropical conditions as indicator of the general health of the colony. *Sociobiology* 67(4):545–553. <https://doi.org/10.13102/sociobiology.v67i4.4926>
- Byatt MA, Chapman NC, Latty T, Oldroyd BP (2016) The genetic consequences of the anthropogenic movement of social bees. *Insectes Soc* 63(1):15–24
- Camargo JMF, Moure JS (1988) Notas sobre Meliponinae (Hymenoptera, Apidae) colecionados por Filippo Silvestri na bacia do Rio da Prata *Rev Bras Entomol, Curitiba* 32(2):293–314
- Camargo JMF, Pedro SRM (2013) Meliponini Lapeletier, 1836, in: Moure, J. S., Urban, D. and Melo, G. A. R. (Eds), *Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region* <http://www.moure.cria.org.br/catalogue> (Accessed on 05 July 2021)
- Campbell AJ, Carnevalheiro LG, Maués MM, Jaffé R, Giannini TC, Freitas MAB, Coelho BWT, Menezes C (2018) Anthropogenic disturbance of tropical forests threatens pollination services to açai palm in the Amazon river delta. *J Appl Ecol* 55:1725–1736. <https://doi.org/10.1111/1365-2664.13086>
- Carmo-Filho FD, Espínola-Sobrinho J, Maia-Neto JM (1991) Dados climatológicos de Mossoró: um município semi-árido nordestino. *ESAM, Mossoró*
- Cortopassi-Laurino M, Imperatriz-Fonseca VL, Roubik DW, Dollin A, Heard T, Aguilar I, Venturieri GC, Eradley C, Nogueira-Neto P (2006) Global meliponiculture: challenges and opportunities. *Apidologie* 37(2):275–292. <https://doi.org/10.1051/apido:2006027>
- Felix JA, Freitas BM (2021) Richness and distribution of the meliponine fauna (Hymenoptera: Apidae: Meliponini) in the State of Ceará, Brazil *An Acad Bras Cienc*. <https://doi.org/10.1590/0001-3765202120190767>
- Freitas BM, Imperatriz-Fonseca VL, Medina LM, Kleinert AMP, Galetto L, Nates-Parra G, Quezada-Euán JGG (2009) Diversity, threats and conservation of native bees in the Neotropics. *Apidologie* 40(3):332–346. <https://doi.org/10.1051/apido/2009012>
- Funceme - Fundação Cearense de Meteorologia e Recursos Hídricos (2019) Recursos Hídricos. <http://www.funceme.br> (Accessed on 05 July 2021)
- Giannini TC, Boff S, Cordeiro GD, Cartolano EA, Veiga AK, Imperatriz-Fonseca VL, Saraiva AM (2015) Crop pollinators in Brazil: a review of reported interactions. *Apidologie* 46:209–223. <https://doi.org/10.1007/s13592-014-0316-z>
- Hill R, Nates-Parra G, Quezada-Euán JGG, Buchori D, LeBuhn G et al (2019) Biocultural approaches to pollinator conservation. *Nat Sustain* 2:214–222. <https://doi.org/10.1038/s41893-019-0244-z>
- Ihering H (1932) A uruçu na apicultura nordestina. *Chác Quintais* 46:292–296
- Imperatriz-Fonseca VL, Koedam D, Hrncir M (eds) (2017) *A abelha jandaíra no presente, no passado e no futuro*. Edufersa, Mossoró, pp 185–199
- Jaffé R, Pope N, Carvalho AT, Maia UM, Blochtein B, Carvalho CAL et al (2015) Bees for development: Brazilian survey reveals how to optimize stingless beekeeping. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0121157>
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proc Royal Soc b* 274(1608):303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Leão KL (2019) *Desenvolvimento colonial em abelhas nativas sem ferrão Amazônicas (Apidae: Meliponini): Tamanho populacional, nutrição e alocação fenotípica*. PhD Thesis, UFPA, Belém
- Maia UM, Jaffé R, Carvalho AT, Fonseca VLI (2015) Meliponiculture in Rio Grande do Norte. *Braz J Vet Med* 37(4):327–333
- Maia UM, Miranda LS, Carvalho AT, Imperatriz-Fonseca VL, Oliveira GC, Giannini TC (2020) Climate-induced distribution dynamics of *Plebeia flavocincta*, a stingless bee from Brazilian tropical dry forests. *Ecol Evol* 10:10130–10138. <https://doi.org/10.1002/ece3.6674>
- Martins CF, Laurino MC, Koedam D, Imperatriz-Fonseca VL (2004) Espécies arbóreas utilizadas para nidificação por abelhas-sem-ferrão na caatinga (Seridó,

- PB; João Câmara, RN). *Biota Neotrop* 4(2):1–8. <https://doi.org/10.1590/S1676-06032004000200003>
- Michener, C. D. (2007) *The bees of the world*. 2nd Edition, John Hopkins University Press, Baltimore
- Moure JS (2004) Duas espécies novas de *Plebeia* Schwarz do Brasil (Hymenoptera, Apidae, Meliponinae). *Revista Brasileira De Entomologia* 48(2):199–202. <https://doi.org/10.1590/S0085-56262004000200007>
- Nogueira-Neto, P (1997) Vida e criação de abelhas indígenas sem ferrão. São Paulo, Brazil
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120(3):321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Pedro SR (2014) The stingless bee fauna in Brazil (Hymenoptera: Apidae). *Sociobiology* 61(4):348–354. <https://doi.org/10.13102/sociobiology.v61i4.348-354>
- Pick RA, Blochtein B (2002) Atividades de vôo de *Plebeia saiqui* (Holmberg) (Hymenoptera, Apidae, Meliponini) durante o período de postura da rainha e em diapausa. *Rev Bras Zool* 19:827–839. <https://doi.org/10.1590/S0101-81752002000300021>
- Potts SG, Imperatriz-Fonseca VL, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ (2016) Safeguarding pollinators and their values to human well-being. *Nature* 540(7632):220–229. <https://doi.org/10.1038/nature20588>
- Ribeiro MF, Imperatriz-Fonseca VL, Filho PSS (2003) A interrupção da construção de células de cria e postura em *Plebeia remota* (Holmberg) (Hymenoptera, Apidae, Meliponini), in: Melo, G. A. R. and Alves-Dos-Santos, I. (Eds.), *Apoidea Neotropica: homenagem aos 90 anos de Jesus Santiago Moure*. Editora UNESC, Criciúma 177–188
- Ribeiro MDF, Taura TA (2019) Presence of *Plebeia* aff. *flavocincta* nests in urban areas. *Sociobiology* 66(1):66–74. <https://doi.org/10.13102/sociobiology.v66i1.3474>
- Roubik DW (2006) Stingless bee nesting biology. *Apidologie* 37:124–143. <https://doi.org/10.1051/apido:2006026>
- Roubik DW (2013) Why do they keep changing the names of our stingless bees (Hymenoptera: Apidae; Meliponini)? A little history and guide to taxonomy, in: Vit P. and Roubik D. W. (Eds.), *Stingless bees process honey and pollen in cerumen pots*. Universidad de Los Andes; Mérida 1–7
- Sanches MA, Pereira MAS, Serrão JE (2017) Pharmacological actions of extracts of propolis of stingless bees (Meliponini). *J Apicultural Res* 56(1):50–57 <https://doi.org/10.1080/00218839.2016.1260856>
- Santos CF, Nunes-Silva P, Blochtein B (2016) Temperature rise and its influence on the cessation of diapause in *Plebeia droryana*, a eusocial bee (Hymenoptera: Apidae). *Ann Entomol Soc Am* 109:29–34. <https://doi.org/10.1093/aesa/sav096>
- Santos CF, Acosta AL, Halinski R, de Souza dos Santos PD, Borges RC, Gianinni TC, Blochtein B (2022) The widespread trade in stingless beehives may introduce them into novel places and could threaten species. *J Appl Ecol*. <https://doi.org/10.1111/1365-2664.14108>
- Santos WO, Mesquita FO, Batista BD, Batista RO, Alves AS (2014) Precipitações máximas para o município de Mossoró de 1964 a 2011 pela distribuição de gumbel. *Irriga* 19(2):207–213. <https://doi.org/10.15809/irriga.2014v19n2p207>
- Silva APV, Alencar MCB, Maracajá PB, Cabral SAAO, Silveira DC, Carmo ES (2015) Atividade antifúngica do mel de abelha *Plebeia* cf. *flavocincta* contra *Aspergillus niger*. *Acta Apic Bras* 3(1),1–9. <https://doi.org/10.18378/aab.v3i1.3500>
- Silva JB, Costa KM, Coelho WA, Paiva KA, Costa GA, Salatino A, Freitas C, Batista JS (2016) Quantificação de fenóis, flavonoides totais e atividades farmacológicas de geoprópolis de *Plebeia* aff. *flavocincta* do Rio Grande do Norte. *Pesq Vet Bras* 36(9), 874–880. <https://doi.org/10.1590/S0100-736X2016000900014>
- Silveira FS, Melo GAR, Almeida EAB (2002) *Abelhas Brasileiras, Sistemática e Identificação*. Author's Edition, Belo Horizonte
- Suka T, Inoue T (1993) Nestmate recognition of the stingless bee *Trigona (Trigona) minangkabau* (Apidae, Meliponini). *J Ethol* 11:141–147. <https://doi.org/10.1007/BF02350047>
- Werneck HDA (2016) *Sistemática molecular e evolução do clado Plebeia: análises baseadas em filogenia e datação molecular da tribo Meliponini*. PhD Thesis. Universidade Federal de Viçosa, Viçosa
- Wiens JJ (2011) The niche, biogeography and species interactions. *Phil Trans R Soc B* 366:2336–2350. <https://doi.org/10.1098/rstb.2011.0059>
- Wille A (1983) Biology of the stingless bees. *Ann Rev Entomol* 28:41–64. <https://doi.org/10.1146/annurev.en.28.010183.000353>
- Witter S, Blochtein B, Andrade F, Wolff LF, Imperatriz-Fonseca VL (2007) Meliponicultura no Rio Grande do Sul: contribuição sobre a biologia e conservação de *Plebeia nigriceps* (Friese 1901) (Apidae, Meliponini). *Biosci J* 23:134–140
- Wittmann, D (1989) Nest architecture, nest site preferences and distribution of *Plebeia wittmanni* (Moure & Camargo, 1989) in Rio Grande do Sul, Brazil (Apidae: Meliponinae). *Studies on Neotropical Fauna and Environment* 24(1):17–23. <https://doi.org/10.1080/01650528909360771>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.