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TAXONOMÍA

Synopsis of the stingless bees of the *favosa* group of the genus *Melipona* (Hymenoptera: Apidae: Meliponini) in Colombia

Sinopsis de las abejas sin aguijón del grupo *favosa* del género *Melipona* (Hymenoptera: Apidae: Meliponini) en Colombia

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ABSTRACT

Stingless bees (Apidae: Meliponini) are of great biological, economic, and culturally important group. In Colombia, species such as those of the *favosa* group of the genus *Melipona* with three species reported for the country especially stand out. However, these species have been traditionally differentiated based on the coloration of the integument, which is a highly variable character in individuals of the same species. On the other hand, the characters of the associated sterna, which are of taxonomic importance in the group, have never been reviewed. In this research, we studied the species of the *favosa* species group known for Colombia. We reviewed 377 individuals of the *favosa* group from different biogeographic regions where individuals have been reported, and we also reviewed the characters associated to coloration of the integument and the male terminalia of the specimens examined. Our results indicated that the characters of coloration traditionally used to separate the species were not consistent; we observed high variation even in individuals from the same nest. We also found that the sterna of males from different biogeographic regions did not differ from each other; however, they did differ from the sterna of *M. orbignyi* from Argentina and thus, bear characters of taxonomic importance for the group. These results indicate that the *favosa* group in Colombia is represented by a single species, *Melipona favosa*.

Keywords: Apinae, Cargabarro, Corbiculated bees, Meliponiculture, Morphology, Stingless bees.

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RESUMEN

Las abejas sin aguijón (Apidae: Meliponini) son un grupo de gran importancia biológica, económica y cultural. En Colombia destacan especies como las del grupo *favosa* del género *Melipona* con tres especies reportadas para el país. Sin embargo, las especies de este grupo han sido tradicionalmente diferenciadas a partir de la coloración del integumento, carácter altamente variable individuos de una misma especie. Por otro lado, los caracteres de los esternos asociados, los cuales son de importancia taxonómica en el grupo, nunca han sido revisados. En este trabajo se estudiaron las especies del grupo *favosa* presentes en Colombia, se revisaron 377 individuos del grupo *favosa* de las distintas regiones biogeográficas donde el grupo ha sido reportado, de igual forma, también se revisaron los caracteres asociados a la coloración del integumento y de la terminalia masculina de los ejemplares examinados. Nuestros resultados indican que los caracteres de coloración tradicionalmente utilizados para separar las especies no fueron consistentes y presentaron una alta variación inclusive en individuos de un mismo nido. También se encontró que los esternos de los machos provenientes de las distintas regiones biogeográficas no presentaban diferencias entre sí, sin embargo, estos si difieren de los esternos de *M. orbignyi* de Argentina, teniendo caracteres de importancia taxonómica para el grupo. Estos resultados indican que el grupo *favosa* en Colombia se encuentra representado por una única especie, *Melipona favosa*.

Palabras clave: Abejas corbiculadas, Apinae, Abejas sin aguijón, Cargabarro, Meliponicultura, Morfología.

INTRODUCTION

The tribe Meliponini, also known as stingless bees, has a pantropical distribution and comprises about 550 currently described species. The highest diversity is concentrated in the Neotropical region with 426 species (76 %) (Grüter 2020). Stingless bees are considered one of the most important pollinator groups for tropical flora (Momose *et al.* 1998, Heard 1999, Michener 2007, Absy *et al.* 2018, Toledo-Hernández *et al.* 2022), as they make up about 50 % of the melittofauna of the tropics (Cairns *et al.* 2005, Brosi *et al.* 2007, Gutiérrez-Chacón *et al.* 2018) and provide benefits to about 100 species of agriculturally important crops (Heard 1999, Giannini *et al.* 2015, Grüter 2020).

Stingless bees also represent a socioeconomic component for many human communities around the world, where they are used to obtain honey, waxes, and propolis, this is an activity known as meliponiculture or stingless beekeeping (Cortopassi-Laurino *et al.* 2006, Kwapong *et al.* 2010, Nates-Parra and Rosso-Londoño 2013, Quezada-Euán 2018). The genera *Tetragonisca* Moure, 1946, and *Melipona* Illiger, 1806 are the most used in meliponiculture in the Neotropics (Alves 2013). However, in terms of production, a *Tetragonisca* nest produces about one kg of honey annually (Carvalho *et al.* 2003), while some *Melipona* species produce 15–25 kg (Kerr *et al.* 1967a, Alves 2013). In Colombia *Melipona* is the genus with the greatest number of species used in meliponiculture (Nates-Parra and Rosso-Londoño 2013), and the genus is the second with the largest number of species reported for the country, surpassed by the genus *Trigona* Jurine, 1807 (Flórez *et al.* 2023).

Melipona is a genus that consists of large to medium-sized bees with 74 currently described species (Camargo *et al.* c2023). The most complete taxonomic review of the genus was made by Schwarz (1932), who proposed an identification key to the species described up to that time. In later research, *Melipona* species were grouped into subgenera (Moure 1975, 1992, Silveira *et al.* 2002, Melo 2021, Engel 2021), of which the subgenus *Melipona* comprises thirteen species (Table 1) (Camargo *et al.* c2023) that have morphological characters that allow them to be easily differentiated from the rest of the subgenera (Silveira *et al.* 2002, Melo 2021, Engel 2021). Within this subgenus, different authors have proposed the *favosa* species group with nine species (Table 1) (*e.g.*, Schwarz 1932, Kerr *et al.* 1967b, Camargo *et al.* 1988) which differs to others species in the

subgenus by the longer interorbital distance at the level of the ocellus with respect to the total length of the eye, giving the appearance of a broad head; the lack of maculations in mesoscutum, axillae and in the medial region of T1; and the punctation of the clypeus.

The *favosa* species group of *Melipona* in Colombia is distributed and used in meliponiculture in the Magdalena, Caribbean, and Orinoco plains (Nates-Parra 2001, Nates-Parra and Rosso Londoño 2013, Gonzalez *et al.* 2021, Camargo *et al.* c2023, Ascher and Pickering c2024). These bees have been persecuted for the exploitation of resources, such as honey and wax (Nates-Parra and González 2000) which led to species such as *Melipona favosa* (Fabricius, 1798) being considered a Vulnerable (VU) category species according to IUCN criteria (Nates-Parra 2007), however, the distributional range of this species is expected to expand in the future (Gonzalez *et al.* 2021).

Nates-Parra and Roubik (1990) recognizes the presence of *M. favosa*, *Melipona orbignyi* (Guérin, 1844), and "*Melipona* new form" in Colombia; later, Nates-Parra (1995, 2001) reports the first two and *Melipona phenax* Cockerell, 1919. However, Camargo *et al.* (c2023) question the presence of *M. orbignyi* because it is a southern South American species, and they only list the presence of *M. favosa* and *M. phenax* in Colombia, the latter restricted to Cundinamarca (Table 1).

Nates-Parra and Roubik (1990) discard the use of genital characters to differentiate the species because "no differences were found in the size or shape of the genitalia of four males of *Melipona favosa* from Panama, Argentina or the two varieties from Colombia". Therefore, only characters associated with the coloration of the integument are used to differentiate the species of this group, like the clypeus as proposed by Schwarz (1932) and metasomal bands.

However, the coloration of the integument in meliponines is a highly variable character in individuals of the same species (Moure 1971, Pedro and Camargo 2003, Engel 2022b), even in individuals of the same nest (Wille 1964, Camargo and Pedro 2003). Likewise, in Nates-Parra and Roubik (1990) only the morphological characters of the genital capsule were considered, discarding other structures with similar taxonomic relevance such as the associated sterna of the genital capsule (Pedro and Camargo 2003, Michener 2007, González and Roubik 2008, Jaramillo *et al.* 2019).

Here, we studied the species of the *favosa* group of *Melipona* in Colombia, using morphological characters of males and females from different biogeographic regions. We propose that the *favosa* species group in Colombia is represented by a single species *M. favosa*; finding that integument color, which is a character traditionally used to separate the species of the group, is highly variable, even in workers of the same nest.

MATERIALS AND METHODS

To generate the occurrence map, we used the locality data associated with specimen labels, as well as those associated to the bibliographic records obtained through the GBIF platform (GBIF c2023). The specimen data without associated coordinates were georeferenced looking for the closest possible locality, using Google Earth (Google, Mountain View). Literature data that did not have a specific locality or a reliable taxonomical identification were excluded from the study. The map was generated with SimpleMappr (Shorthouse 2010).

We studied the following entomological collections:

LABUN: Laboratorio de Abejas de la Universidad Nacional de Colombia (R. Ospina).
ICN-Ent: Colección Nacional de Insectos, Instituto de Ciencias Naturales – Universidad Nacional de Colombia (F. Fernández).
IAvH-E: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt – Colección de Entomología (J. Neita).

The terminology of the morphological structures studied followed Michener (2007). We dissected the male terminalia and placed it in a 10 % KOH solution for 24 hours at room temperature, later it was neutralized with acetic acid. As many morphological characters as possible were examined, including those traditionally used in the literature to recognize the different *Melipona* taxa (Supp. Table 1). We also examined the shape, pilosity and position of spiracles of associated sterna seven (S7) as proposed by Camargo *et al.* (1988), because those characters have a particular taxonomical importance in stingless bees (Camargo *et al.* 1988, Pedro and Camargo 2003, Camargo and Pedro 2004, Jaramillo *et al.* 2019). Characters were studied using a Leica MZ6 steromicroscope. We photographed specimens with an Olympus OM-D E.M1 II camera mounted vertically on a MENGS PU-140 and

Table 1: Distribution of the *favosa* species group and *Melipona* species reported for Colombia. Data obtained from Camargo *et al*. (c2023) and Flórez *et al*. (2023). * The records of *M. favosa* form Brazil were obtained in GBIF (c2023), however these specimens were not studied and this species does not have records for Brazil neither in Camargo *et al*. (c2023) nor Ascher and Pickering (c2024).

Species	Author	Distribution
Species of *Melipona* (*Melipona*) not belonging to *favosa* species group		
Melipona asilvai	Moure, 1971	Brazil
Melipona lupitae	Ayala, 1999	Mexico
Melipona quadrifasciata	Lepeletier, 1836	Argentina, Brazil and Paraguay
Melipona yucatanica	Camargo, Moure & Roubik, 1988	Costa Rica, Guatemala and Mexico
Species of *Melipona* (*Melipona*) belonging to *favosa* species group		
Melipona baeri	Vachal, 1904	Argentina and Bolivia
Melipona lunulata	Friese, 1900	Bolivia
Melipona orbignyi	(Guérin, 1844)	Argentina, Bolivia, Brazil, and Paraguay
Melipona peruviana	Friese, 1900	Peru
Melipona phenax	Cockerell, 1919	Ecuador and Panama
Melipona variegatipes	Gribodo, 1893	Dominica, Guadeloupe, and Montserrat
Melipona mandacaia	Smith, 1863	Brazil
Melipona subnitida	Ducke, 1910	Brazil
Melipona favosa	(Fabricius, 1798)	Colombia, *Brazil, French Guiana, Venezuela, Guyana, Suriname, and Trinidad and Tobago
Species of *Melipona* reported for Colombia		
Melipona ambigua	Roubik & Camargo, 2012	Colombia
Melipona bradleyi	Schwarz, 1932	Brazil and Colombia
Melipona captiosa	Moure, 1962	Brazil, Colombia, Guiana and Suriname
Melipona compressipes	(Fabricius, 1804)	Brazil, Colombia, French Guiana, Guiana, Suriname, and Venezuela
Melipona costaricensis	Cockerell, 1919	Costa Rica and Colombia
Melipona cramptoni	Cockerell, 1920	Brazil, Colombia, Guiana, and Venezuela
Melipona fallax	Camargo & Pedro, 2008	Colombia, Costa Rica, Ecuador, Nicaragua, and Panama
Melipona favosa	(Fabricius, 1798)	Colombia, *Brazil, French Guiana, Venezuela, Guyana, Suriname, and Trinidad and Tobago
Melipona fulva	Lepeletier, 1836	Brazil, French Guiana, Guiana, Suriname, Venezuela, and Colombia
Melipona fuscopilosa	Moure & Kerr, 1950	Brazil, Colombia and Peru
Melipona grandis	Guérin, 1844	Bolivia, Brazil, Colombia, Ecuador, and Peru
Melipona indecisa	Cockerell, 1919	Colombia and Venezuela
Melipona nebulosa	Camargo, 1988	Bolivia, Brazil and Colombia
Melipona nigrescens	Friese, 1900	Colombia
Melipona panamica	Cockerell, 1912	Colombia, Costa Rica, and Panama
Melipona salti	Schwarz, 1932	Colombia
Melipona titania	(Gribodo, 1893)	Argentina, Brazil, Colombia, Ecuador, and Peru.

MENGS CL-120 quick-release rail mount and controlled using OM Capture software. Photo stacking was made using Helicon Focus 8.1.0 software and final images were edited using Photoshop CS6 (PSC6). We used the following symbols: workers (♀), males (♂), and queens (☿).

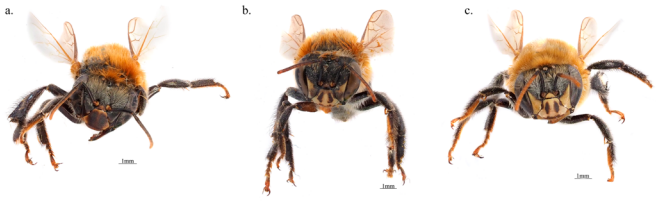

Figure 1: Workers from the three biogeographic regions: **(a.)** Magdalena region (Huila, Rivera), *Melipona favosa* (dark form) LABUN31200. **(b.)** Caribbean region (Magdalena, Taganga), *Melipona favosa* (intermediate form) LABUN28805. **(c.)** Orinoco region (Casanare, Trinidad), *Melipona favosa* (light form) LABUN35085.

We confirmed taxonomic identities with photos of type specimens (Supp. Fig. 1–3): lectotype of *Melipona favosa* from the University of Copenhagen Zoological Museum (ZMUC); holotype of *Melipona phenax* from the Smithsonian Institution (USNM) website (https://collections.nmnh.si.edu/search/ento/); and for *Melipona orbignyi* we requested photographs of the holotype and topotype to Leopoldo Álvarez of the Universidad de la Plata (MLP), both specimens deposited in the Muséum national d'histoire naturelle (MNHP).

RESULTS

Systematics

***Melipona* Illiger, 1809**

***Melipona* (*Melipona*) Illiger, 1809**

***Melipona favosa* (Fabricius, 1798)**

Apis favosa Fabricius, 1798

Material examined: (n=348♀, 22♂, 7☿). (Supplementary material 2)

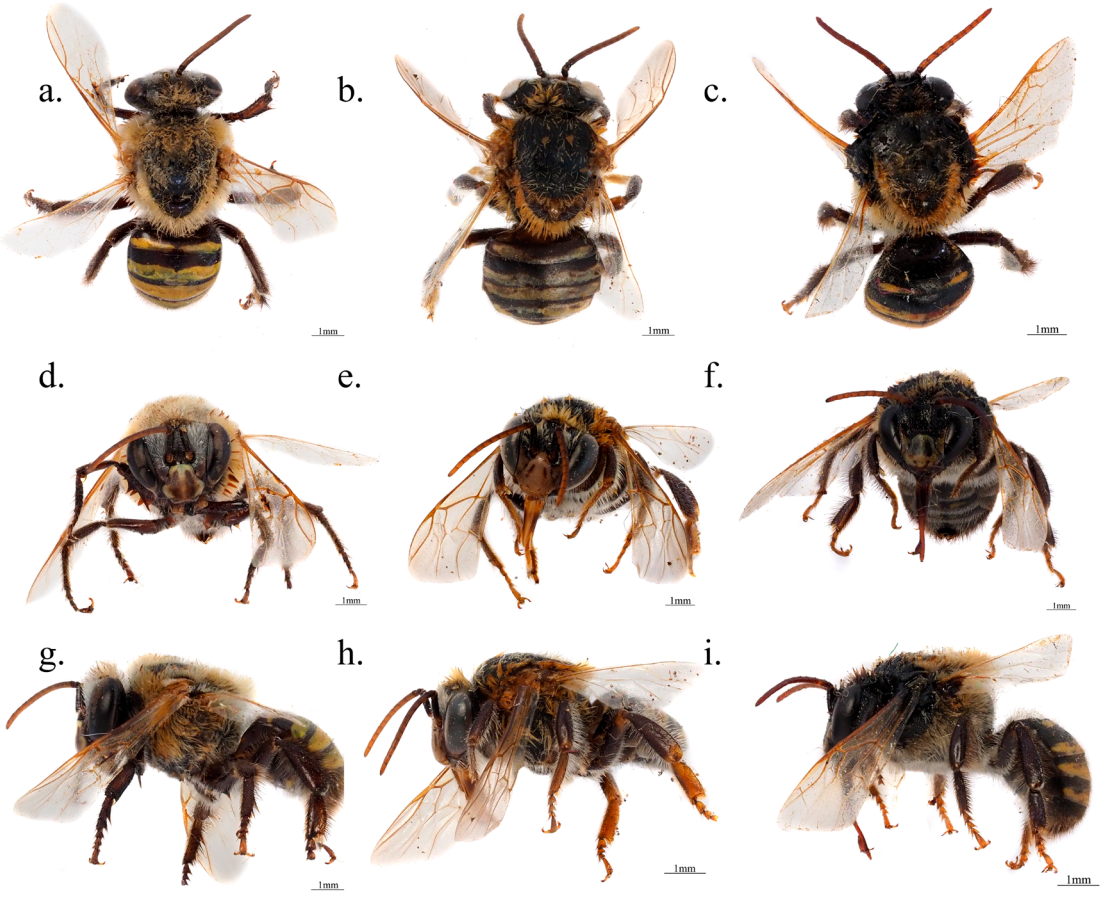

Figure 2: Males from the three biogeographic regions. (**a–c**) Dorsal view, (**d–f**) frontal view, and (**g–i**) lateral view. (**a, d** and **g**) Magdalena region (Tolima, Ambalema), *Melipona favosa* (dark form) LABUN3401. (**b**, **e** and **h**) Orinoco region (Cundinamarca, Paratebueno), *Melipona favosa* (light form) LABUN3415. (**c**, **f** and **i**) Caribbean region (Atlántico, Barranquilla), *Melipona favosa* (light form) LABUN21109.

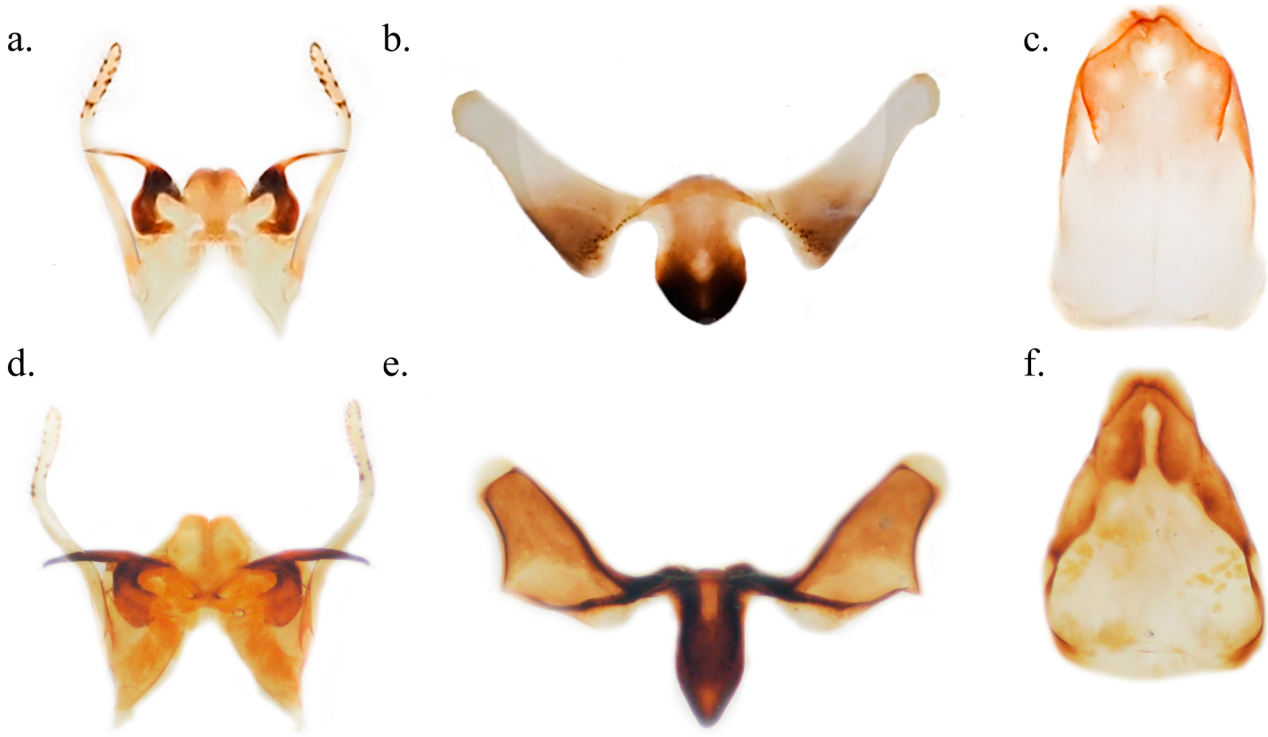

Figure 3: Terminalia: (**a–c**) *Melipona favosa* (Ambalema, Tolima, Colombia). (**d–f**) *Melipona orbignyi* (Campo Gallo, Santiago del Estero, Argentina). (**a** and **d**) Genital capsule in schizogonal disposition, (**b** and **e**) S7 and (**c** and **f**) S8.

Morphological identification

The integument coloration characters that Schwarz (1932) and Nates-Parra and Roubik (1990) propose to differentiate the species of *M. favosa* and *M. phenax,* were found throughout the country with light forms and dark forms (Fig.1, 2), including individuals from the same nest (Fig. 4). The pilosity, structure punctuation or sculpturing of none of the specimens examined showed evident differences in any of the three biogeographic regions studied. Similarly, both workers and males had reddish or fulvous pilosity on the vertex (Fig. 1, Fig. 4) and white or light pilosity on the lateral region of the terga (Fig. 2, Fig. 6). However, the pilosity in the lateral region of the terga of the Colombian specimens differs from the pilosity of *M. orbignyi* which is completely or mostly black (Supp. Fig. 3).

The genital capsules, S7 and S8 are similar in males from all biogeographic regions. There were no clear differences in the disposition of the gonostylus, nor the shape and pilosity of the gonocoxite, penis valves, spathes, S7 and S8 (Supp. Fig. 4-5). However, the shape of the S7 and S8 of the specimens from Colombia differs from the specimen of *M. orbignyi* from Argentina (Fig. 3). Finally, both the genital capsule and S8 of *M. favosa* were similar to *M. phenax* reported by Schwarz (1932), S6 and S7 were not reviewed in this work.

Distribution

Melipona favosa is a species that occurs in northern South America in the following countries: Colombia, French Guiana, Venezuela, Guyana, Suriname, and Trinidad and Tobago. In Colombia, this species can be found in the biogeographic regions of the Caribbean, Savanna, and Magdalena proposed by Morrone (2014), at altitudes ranging from sea level to 1443 m above sea level (Fig. 5).

DISCUSSION

The tribe Meliponini in Colombia is represented by 23 genera (Flórez *et al.* 2023), of which only fourteen have been reviewed in the current taxonomical literature (Camargo and Moure 1994, Camargo and Moure 1996, González-B and

Nates-Parra 1999, Camargo and Pedro 2002, González and Smith-Pardo 2003, Camargo and Pedro 2003, 2004, Camargo and Roubik 2005, González and Roubik 2008, Gonzalez and Engel 2012, Jaramillo *et al.* 2019, Nogueira *et al.* 2019, Guevara *et al.* 2020, Nogueira *et al.* 2020, Engel 2022a, 2022b, 2022c, 2022d, Lepeco 2024). *Melipona* is the largest genus of Meliponini (Melo 2021) however, its taxonomy remains poorly understood and requires a comprehensive modern revision (Flórez *et al.* 2023). After discarding the presence of *M. phenax* and *M. orbignyi* in the country, Colombia currently reports 17 species of the genus (Table 1) with just *M. favosa* belonging to the *favosa* group.

Figure 4: Workers of *Melipona favosa* from the same nest (Specimens from the Caribbean biogeographic region. Sucre, San Onofre): **(a)** Light form LABUN41329. **(b)** Intermediate form LABUN41340. **(c)** Dark form LABUN41328.

The category of species groups within the genus *Melipona* is widely used, as it includes species with evident morphological characters (Schwarz 1932, Moure and Kerr 1950). Some species groups are maintained within the subgenus *Melipona (Michmelia)* Moure, 1975 (Schwarz 1932, Moure and Kerr 1950, Camargo et al. c2023), however others such as the *compressipes* species group are no longer in use because all species fit in the subgenus *Melipona (Melikerria)* Moure, 1992.

The *favosa* species group is no longer used by some authors (Camargo c2023), however it is not clear whether other species of the subgenus can be considered within this species group. Camargo et al. (1988) suggest the inclusion of *Melipona subnitida* Ducke, 1910 within the *favosa* species group, however, species such as *Melipona yucatanica* Camargo, Moure & Roubik, 1988, *Melipona lupitae* Ayala, 1999 or *Melipona quadrifasciata* Lepeletier, 1836 do not share many common characteristics with the *favosa* group, even, species like *Melipona asilvai* Moure, 1971 does not share characteristics of the subgenus (Schwarz 1932, Camargo et al. 1988, Melo 2021, Engel 2021) but it belongs to the subgenus (Ramirez et al. 2010, Lepeco et al. 2024), so a systematic study of the subgenus and the genus as such is necessary.

The distributional pattern of *M. favosa* agrees with other bee species like *Anthidium sanguinicaudum* Schwarz, 1933, *Partamona peckolti* (Friese, 1901), and *Frieseomelitta paupera* (Provancher, 1888) (Pedro and Camargo 2003, Camargo and Pedro 2003, Gonzalez and Griswold 2013, Guevara *et al.* 2022, Camargo *et al.* c2023); these species occur throughout northern South America. In Colombia, *M. favosa* occurs at altitudes ranging from sea level to 1443 m above sea level where there are ecosystems such as tropical dry forests and eastern savannas (Pizano and Garcia 2014, Dryflor *et al.* 2016, González-M *et al.* 2018, Gori *et al.* 2022).

Although many authors use characters of integument coloration to separate Meliponini species, these are usually associated with morphological characters and geographical patterns (Camargo and Moure 1994, Pedro and Camargo 2003, Camargo and Pedro 2003, 2004, González and Roubik 2008, Gonzalez and Griswold 2012). In this study, we found that the coloration of the integument is highly variable, exhibiting different forms of coloration (Moure and Kerr 1950) even coexisting in the same nest, as reported for other meliponines species (Wille 1964, Pedro and Camargo 2003, Engel 2022b). Additionally, we did not find any differences between the lectotype of *M. favosa* examined and the holotype *M. phenax*, so we suggest examining the terminalia of the *M. phenax* male to define the taxonomic status of these species, this is because females differ just by lacking or not the maculation of the face.

The genital capsule of *M. orbignyi* is like that of *M. favosa* (Fig. 3). However, the sterna, S7 and S8, showed relevant differences. The median projection of S7 of *M. favosa* was proportionally wider than that of *M. orbignyi*; the spiracle of *M. favosa* is in the central region of the projection (Fig. 3b), while the spiracle of *M. orbignyi* is located at the proximal margin of the sternum (Fig. 3e). The shape of S8 in *M. favosa* is rectangular shape, with the lateral margin subparallel (Fig. 3c), in *M. orbignyi* the S8 is trapezoidal or triangular, with lateral margins tapering apically (Fig. 3f). This provides further evidence (Pedro and Camargo 2003, Michener 2007, González and Roubik 2008, Jaramillo *et al.* 2019) that characters associated to the male terminalia provided taxonomic information for differentiating species in Meliponini.

Despite our analysis, we observed no significant differences in the specimens from the three biogeographic regions studied, including aspects such as punctation, pilosity,

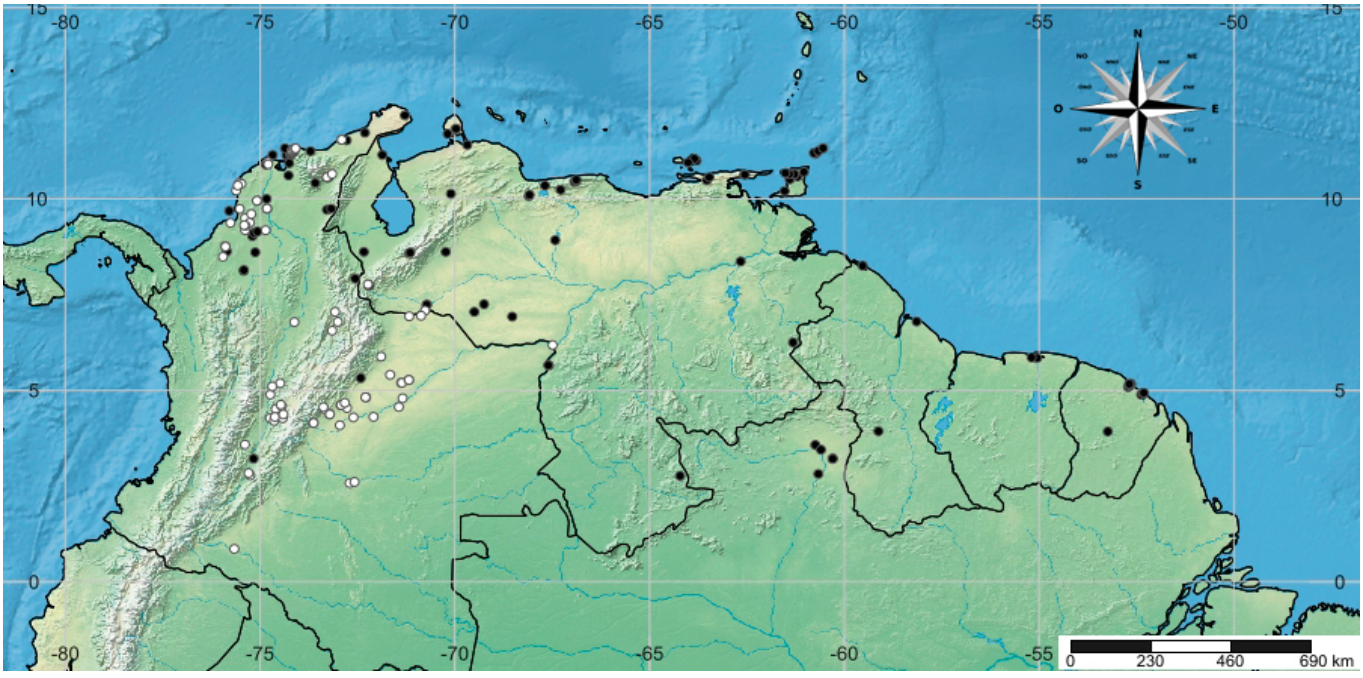

Figure 5: Occurrence records map of *Melipona favosa*. Black dots correspond to bibliographic records. White dots show the material examined.

shape, and even male terminalia (Supp Fig. 4). It is crucial to continue using terminalia associated characters to address many taxonomic questions concerning stingless bees in Colombia, particularly within highly diverse groups like the genus *Melipona*.

Figure 6: Dorsal view of metasoma of *Melipona favosa*.

Although the *favosa* group is represented by a single species in Colombia, relocating colonies is not recommended in the meliponiculture practices for this species or any others. Translocating nests presents a significant risk, as it can also lead to the movement of organisms associated with the nest, such as predators and parasites (Schwarz 1948, Sommeijer 1999, Hernández and Gutiérrez 2001, Rasmussen 2008, Gloag *et al.* 2009, Maia-Silva *et al.* 2013), or even diseases (Guzman-Novoa *et al.* 2015, Shanks *et al.* 2017, Alvarez *et al.* 2018, Teixeira *et al.* 2020), which could negatively impact bee species in other geographic regions.

In Colombia the meliponiculture is primarily supported by regulations related to biodiversity protection, sustainable use of natural resources, and apiculture, there is still missing a specific law that regulate the meliponiculture in the country. We call on the Colombian governmental institutions to create and apply a national policy for meliponiculture in Colombia that prevents the extraction of colonies from the natural environment and the movement of these species between different areas.

CONCLUSIONS

Melipona favosa is the only species of the *favosa* group present in Colombia. *Melipona favosa* has marked differences

in the coloration of the integument, including dark and light forms. This is a highly variable character even in individuals from the same nest. So, using integument coloration as the only character does not allow a good taxonomic resolution, at least in the *favosa* species group. We recommend the use of male terminalia characters and morphological variations and restrict the coloration variation to the pilosity that allows differentiating some species and that is constant in the specimens of *M. favosa* studied.

AUTHOR´S CONTRIBUTIONS

NDGR: Conception and design, identification, material and data curation, illustration, photographs, and writing; ROT: Writing review and editing; DAG: Conception and design, identification, and writing review and editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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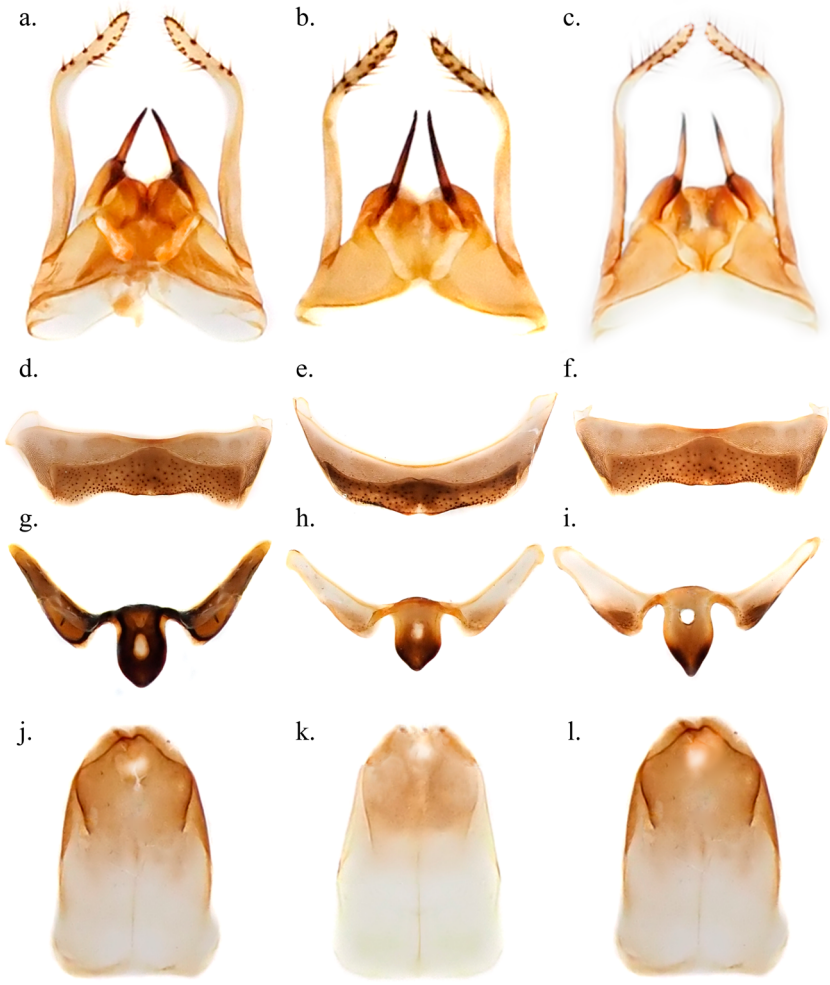
SUPPLEMENTARY MATERIAL 1

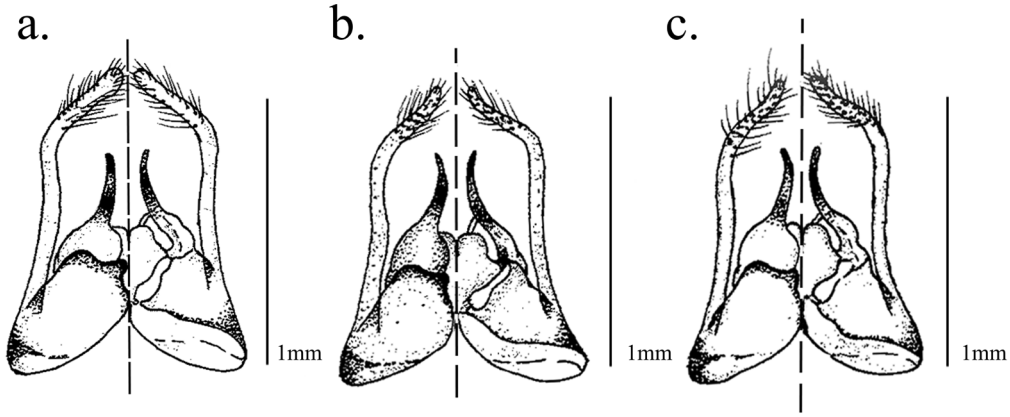
SuppFig. 1: Lectotype of (*Apis favosa* Fabricius, 1798) = *Melipona favosa* (♀): **(a)** Lateral view, **(b)** dorsal view, and **(c)** frontal view.

SuppFig. 2: Holotype of *Melipona phenax* Cockerell, 1919 (♀): **(a)** Lateral view, **(b)** dorsal view, and **(c)** frontal view.

SuppFig. 3: Holotype **(a and b)** and topotype **(c)** of *Melipona orbignyi* (Guérin, 1844) (♀): **(a)** Lateral view, **(b)** frontal view, and **(c)** dorsal view.



SuppFig. 4: Terminalia of males of *Melipona favosa* (Fabricius, 1798) from the three biogeographic regions: **(a–c)** Genital capsule; **(d–f)** S6; **(g–i)** S7, and **(j–l)** S8. **(a, d, g,** and **j)** Magdalena Region; **(b, e, h,** and **k)** Orinoco Region; **(c, f, i,** and **l)** Caribbean Region.



SuppFig. 5: Genital capsules of males of *Melipona favosa* (Fabricius, 1789) from the three biogeographic regions of Colombia. **(a)** Caribbean Region; **(b)** Magdalena region; **(c)** Orinoco region. The left part of each image corresponds to the dorsal view of the capsule, while the right part corresponds to the ventral view.

SuppTable 1: Morphological characters of workers used traditionally to identify *Melipona* taxa.

	Character	Character states	Taxonomic group	References
Pilosity	Vertex	1) Only fulvous or white. 2) Blackish or blackish intermixed with white.	- *M. (Michmelia) fasciata* group.	Schwarz 1932, Engel 2021.
	Clypeus	1) Extremely minute (without evident pilosity). 2) Conspicuous pilosity or with decumbent pubescence. 3) Short and decumbent; sparse composed mostly by simple hairs or dense with a mixture of simple and plumose hairs. 4) Erect and conspicuous; composed by a mixture of simple hairs longer than plumose hairs.	- *M. (Eomelipona)* spp. - *M. (Melipona)* spp. - *M. (Meliponiella)* spp.	Schwarz 1932, Melo 2021.
	Mesosoma	1) Mainly black. 2) Mainly fulvous, ferruginous or white.	- *M. (Melikerria)* spp. - *M. (Meliponiella)*spp. - *M. (Michmelia) fasciata* group. - *M. (Melipona) favosa* group.	Schwarz 1932, Roubik and Camargo 2012.
	Mesoscutum	1) Anterolateral margin of mesoscutum with a dense tuft of reddish plumose hairs. 2) Anterolateral margin of mesoscutum with pilosity of the same color as the mesoscutum disc .	- *M. (Melikerria)* spp.	Schwarz 1932, Roubik and Camargo 2012, Engel 2021, Melo 2021.
	Mesepisternum	1) dorsal region with black pilosity (contrasting with the light pilosity of the rest of the mesepisternum) 2) White or fulvous.	- *M. (Michmelia) fasciata* group.	Schwarz 1932.
	T2	1) Only simple and sparse hairs. 2) Dense and plumose hairs.	- *M. (Michmelia) fuliginosa* group.	Camargo and Pedro 2008.
	Lateral region of terga	1) Blackish (in some species with some white hairs). 2) Whitish or yellowish.	- *M. (Michmelia) fasciata* group. - *M. (Melipona) favosa* group.	Schwarz 1932.
Structure	Malar area	1) As long as or longer than the diameter of flagellum. 2) Shorter than length of the diameter of flagellum.	- *M. (Meliponiella)* spp. - *M. (Eomelipona)* spp. - *M. (Michmelia) fasciata* group.	Schwarz 1932, Melo 2021.
	Superior interocular distance	1) Longer than length of the eye. 2) Shorter or as long as the length of the eye.	- *M. (Melipona) favosa* group.	Schwarz 1932, Camargo et al. 1988.
	Occipital carina (When see from above)	1) Forming a transverse crest behind head. 2) Very low, not forming a crest behind head.	- *M. (Eomelipona)* spp. - *M. (Meliponiella)* spp.	Melo 2021.
	Shape of mandibles	1) Teeth along cutting edge of mandible strong, emargination between basal and second teeth relatively short and deep. 2) Teeth along cutting edge of mandible relatively small, emargination between basal and second teeth shallow.	- *M. (Melikerria)* spp.	Schwarz 1932, Roubik and Camargo 2012, Engel 2021, Melo 2021.
	Penicillium	1) Without conspicuous narrowing at base and simple curved posterior bristles. 2) With a conspicuous narrowing at base and posterior bristles strongly sinuous.	- *M. (Michmelia) fuliginosa* group.	Camargo and Pedro 2008.

	Character	Character states	Taxonomic group	References
Coloration	Mesoscutum	1) With prominent, broad yellow maculation along lateral margins. 2) Without any maculation.	- *M. (Eomelipona)* spp. - *M. (Meliponiella)* spp.	Engel 2021.
	Propodeum	1) With yellow longitudinal lateral stripes. 2) Propodeum without any maculation.	- *M. (Meliponiella)* spp.	Engel 2021, Melo 2021.
	Legs	1) Mainly black. 2) Mainly fulvous or ferruginous.	- *M. (Michmelia) fasciata* group. - *M. (Melipona) favosa* group.	Schwarz 1932.
	Metasoma	1) Banded. 2) Without bands.	- *M. (Eomelipona)* spp. - *M. (Melikerria)* spp. - *M. (Meliponiella)* spp. - *M. (Michmelia) fasciata* group. - *M. (Melipona) favosa* group.	Schwarz 1932, Camargo et al. 1988, Nates-Parra and Roubik 1990, Roubik and Camargo 2012.
Punctation and sculpturing	Clypeus	1) Integument of the clypeus smooth and shiny. 2) Integument of the clypeus dull.	- *M. (Melipona)* spp. - *M. (Michmelia) fuliginosa* group.	Schwarz 1932, Camargo and Pedro 2008, Engel 2021, Melo 2021.
	Mesepisternum	1) Integument dull and dense punctures. 2) Integument shiny and sparse punctures.	- *M. (Eomelipona)* spp. - *M. (Meliponiella)* spp.	Schwarz 1932.